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THE COMPOSITION AND DYNAMICS OF A BEECH-MAPLE CLIMAX COMMUNITY[1]

By

ARTHUR B. WILLIAMS

Cleveland Museum of Natural History

[1] Contribution from the Biological Laboratory of Western Reserve University.

CONTENTS

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INTRODUCTION

The approach in this study is to the biotic community as a whole. It is sought to determine both its plant and animal content; the number and abundance of species; their relations to each other and to the community as a whole; seasonal and yearly variations in numbers and activities; territorial relations; food relations; the stage of succession represented; changes now going on; environmental conditions, including soil and climatic factors; and the effect of these upon the community.

Special emphasis is laid upon the vertebrates and the major plant forms. While it has not been possible to treat the invertebrate life as fully as the plants and vertebrates, some invertebrates have been noted, and are included in this paper.

The writer desires here to acknowledge his indebtedness and to express his appreciation to the Cleveland Metropolitan Park Board for the opportunity afforded for this study within the Cleveland Metropolitan Park System, and for many courtesies extended by park officials; to the Cleveland Museum of Natural History for making this study possible as a piece of research in connection with its program, and to Mr. Harold L. Madison, Director of the Museum, for encouragement in it; to Dr. J. Paul Visscher, Chairman of the Department of Biology of Western Reserve University, for the privilege of coördinating a study of this kind with the regular work of the Department, and especially to Dr. S. C. Kendeigh, of the Department of Biology of Western Reserve University, for his many helpful suggestions and criticisms during the progress of the work and the preparation of this paper.

The writer's thanks are also due to Dr. Addie E. Piehl of the Department of Biology of Western Reserve University for aid in identifying mosses, lichens, and algae; and to Mr. Henry M. Beardslee, of North Perry, Ohio, for similar aid in identifying fungi. To Mr. B. P. Bole, Jr., mammologist of the Cleveland Museum of Natural History, and to Dr. Harry C. Oberholzer, of the United States Biological Survey, the writer is indebted for checking the lists of mammals and of birds, respectively, with special reference to subspecies names. To Mr. Arthur B. Fuller, of the Cleveland Museum of Natural History, to whose expert marksmanship the collection of all of the bats taken in the area is due (for which special permission was given by the Park Board for the purposes of this study), the writer is also indebted. To Mr. Philip Moulthrop, also of the Cleve-

land Museum of Natural History, the writer is indebted for much help in the collection of small mammals.

It is not maintained that this study is now complete. In a sense it might be carried on indefinitely and never be complete. It seems desirable, however, at this time to make available the data thus far collected and to report the findings.

The beech-maple forest (Fagus-Acer association) is an important ecological division of the deciduous forest formation, which formation at the coming of the white man occupied so large a part of the northeastern United States and southern Canada. The deciduous forest has been described by Transeau (1905), Harshberger (1911), Frothingham (1915), Clements (1916), Livingston and Shreve (1921), Shantz and Zon (1924), and Weaver and Clements (1929). Weaver and Clements give the limits of the deciduous forest formation as running on the north from central Minnesota along the south shore of Lake Superior eastward to southwestern Quebec and southern Maine, thence stretching southward into central Georgia, southern Louisiana, and eastern Texas. The same authors regard the beech-maple forest as the "typical association" of the deciduous forest formation, "characterizing its more humid and cooler northern and eastern portions."

The plant structure of the beech-maple association has been studied in detail in southern Michigan by Quick (1923) and by Cain (1935), in northern Michigan by Gleason (1924), and in Indiana by Esten (1932). In Ohio the beech-maple association is emphasized by Sampson (1927) as one of the four primary plant communities in the state on the basis of area covered. Sears (1925), attempting to reconstruct the picture of the natural vegetation of Ohio before the advent of the white man noted that beech, unmixed with oak or ash, was practically limited to the glaciated region of the state. References to the occurrence of both beech and sugar maple throughout their range will be found in the Naturalists' Guide to the Americas, edited by Shelford (1926).

Hemlock is recognized as a frequent constituent of the beech-maple association (Gleason 1924, Weaver and Clements 1929). The hemlock forest has been described by Lutz (1930) and the environmental requirements of hemlock studied by Moore, Richards, Gleason and Stout (1924).

The animal content of the forest, the relationships between plants and animals, and the consideration of the biotic community as such have not thus far been given the consideration accorded to the plant constituents of the community. Important contributions have been made in this country by Adams (1906), Shelford (1913), and Chapman (1931); and in England by Elton (1927, 1930). The mammals of a beech-maple forest in Michigan have been listed by Dice (1920), and an ecological survey of Isle Royale conducted by Adams (1909) included a study of animals found there.

The insect life of an elm-maple forest in Illinois has been studied in detail by Weese (1924), and much the same thing has been accomplished by Blake (1926), working on Mount Katahdin in Maine. A study of the biotic communities of the aspen parklands of central Canada was made by Bird (1930). Shelford and Olsen (1935) have pointed out the relation which animals may have to plant communities as indicators, and maintain that plants and animals are inseparably united in the structure of any community. Much painstaking labor has been devoted to the study of various phases of animal ecology by numerous workers, but there is little in the literature that treats of forest communities as biotic units.

DESCRIPTION OF AREA STUDIED

Location and Physiography

To the northeast of Cleveland, Ohio, and some 16 miles from the city limits, lies the tract of land known as the North Chagrin Reservation of the Cleveland metropolitan park system. It contains 1,201 acres (486.04 hectares), and is roughly rectangular in shape, being approximately a mile and a half (2.41 kilometers) square (Board of Park Commissioners, Report 1932-1933). It lies between parallels 41° 33′ and 41° 35′ north latitude.

The reservation occupies a position at the extreme edge of Appalachian Plateau, as the Portage Escarpment which limits the plateau in this region is represented by the high bluffs of the Chagrin River valley which are a part of the area. The location is well within the boundaries of the advance of the ice sheets of Pleistocene times (Cushing, Leverett, and Van Horn 1931). Lake Erie is distant about 5 miles (8.04 kilometers) in a direct line toward the northwest.

Within the reservation the land slopes gently toward the east for about a mile (1.6 kilometers), where it drops steeply almost to the level of the river. This bluff which marks the border of the valley is deeply and frequently cut by short gullies and ravines only a few of which are extensive enough to carry water all the year. The United States topographical survey map (Mentor Quadrangle) shows the difference in level between the western margin of the reservation and the river to be 220 feet (67.05 meters).

The particular area chosen for this study lies along the southern boundary of the North Chagrin Reservation. It is approximately 65 acres (26.3 hectares) in extent, is entirely wooded, and includes some of the characteristic gullies, ravines, and bluffs of the locality. It does not include any of the river bottom or lower lands. It slopes toward the northeast from 860 feet (262.12 meters) to 760 feet (231.64 meters) above sea level. In outline it is somewhat irregular, because of the nature of the ground, except at its southern and western limits. It is traversed by several foot-trails and

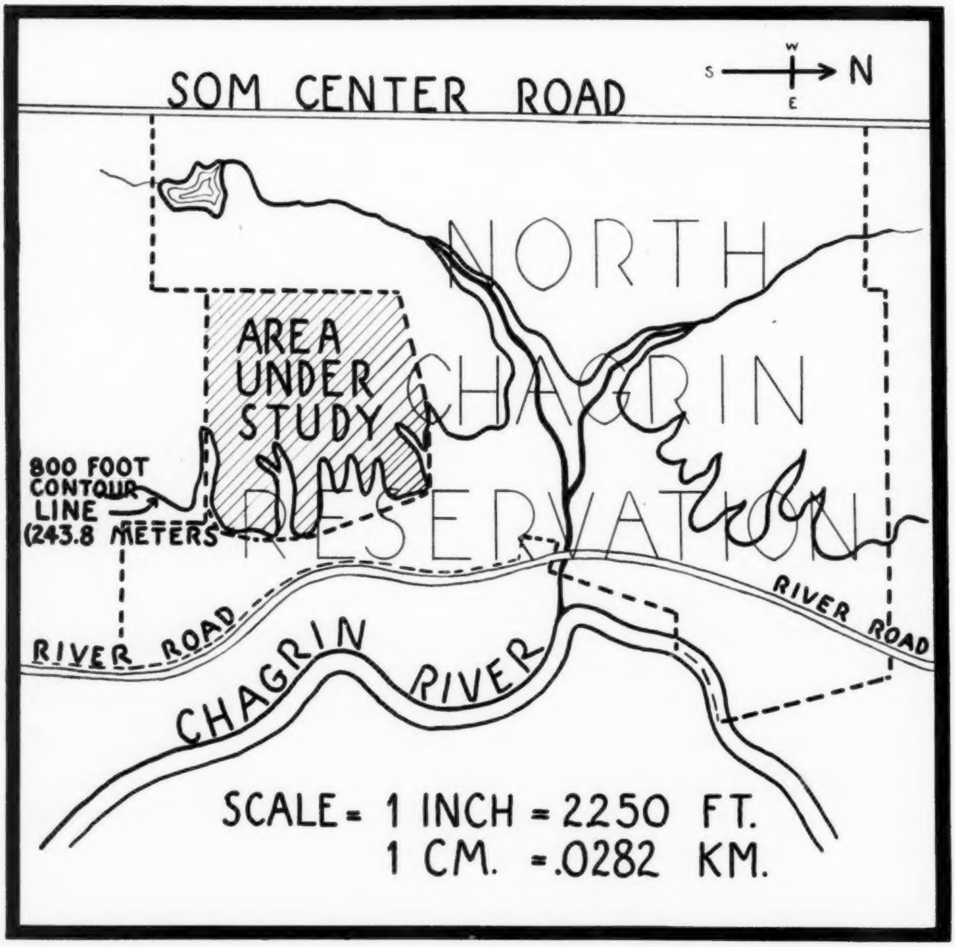

FIG. 1. Map of North Chagrin Reservation showing location of area under study.

bridle-paths which greatly facilitate quiet and easy access to all of its parts. Reference to Figure 1 will give an idea of the topography of the area and of its relation to the entire North Chagrin Reservation. It should be noted that the reservation is not an isolated piece of forest land. While to the west the country is occupied by farms, the adjoining land to the north and south and across the river to the east is largely of the same character as that of the reservation itself.

Geology and Soil

The geological formation immediately underlying the surface soils is that known as the Cleveland Shale. This is a sedimentary rock apparently composed of consolidated black mud (Cushing, Leverett, and Van Horn 1931). Upon this bed-rock of shale a layer of soil of glacial origin known as the Volusia Clay Loam has been deposited. Coffey and Rice (1912), describing this soil, say: "As a general rule, both soil and subsoil are markedly

deficient in lime carbonate, and will redden litmus paper quickly. The Volusia series is derived from glacial deposits of shale and sandstone material which covers the northeastern section of Ohio." The Volusia Clay Loam is a poorly drained soil, and not among the more productive soils of the State. The presence of beech trees is said to be characteristic of the Volusia series. Over the clay loam above described there has been built up a layer of humus of a loose and spongy character from 1 to 4 inches (2.54 to 10.16 cm.) in depth. The clay soil beneath the humus is not more than from 4 to 9 inches (10.16 to 22.86 cm.) deep, but it is friable and porous as compared with the subsoil, which is of dense yellow clay.

Drainage

Because of the heavy quality of the underlying sub-soil, standing water, in hollows, after rains or melting snows, is of common occurrence on the more level parts of the area. Depressions left by the uprooting of large trees will sometimes contain water most of the year if precipitation is fairly regular. In winter and spring the woods of the higher or more westerly part of the area are always wet. Aside from such water as may collect in depressions or pockets, the run-off of excess water is rapid. Within the area there are no constant streams, the waterways with one exception being short and the gradient steep. One waterway, having its collecting basin in the open fields outside the area, and traversing its higher portion in more leisurely fashion, does not become entirely dry except after periods of prolonged drought.

CLIMATE

The close proximity of Lake Erie may be considered as a factor modifying to some extent the climate of the region. In general, as has often been pointed out, temperatures do not rise so high nor fall so low near the lake as they do farther inland. The lake also is often responsible for a condition of cloudiness that cuts down very appreciably the amount of available sunshine (Moseley 1897).

In order to secure positive information as to the factors of temperature, humidity, and precipitation within the area, four stations were established and their operation begun on January 1, 1932. Two of these stations, designated as "A" and "B," were located in beech maple environment. The other two, designated as "C" and "D," were located in beech-hemlock environment. At Station A a hygrothermograph giving continuous records of temperature and relative humidity was installed in a wooden shelter resting on the ground. A rain gauge, by means of which precipitation over a circular area 3 inches (7.62 cm.) in diameter may be measured in hundredths of an inch, was located here. At Stations B, C, and D, maximum and minimum thermometers and rain gauges similar to that at Station A were in-

stalled. The thermometers were secured to the north sides of large trees about 5 feet (1.52 meters) from the ground, and the rain gauges located beneath the same trees from 6 to 10 feet (1.82 to 3.04 meters) from their bases. Readings from all instruments were taken with regularity weekly, and the operation of the hygrothermograph regularly checked as to temperature with a tested thermometer, and as to relative humidity with a cog psychrometer. The thermometers were compared at different temperatures, and their readings found to be in agreement. Their accuracy was also checked with a standard thermometer.

TEMPERATURE

Figure 2 shows the mean temperature by weeks, on the basis of hourly readings, at Station A for the year 1932. To this has been added the records of mean temperature for the same weeks as recorded by the Cleveland Weather Bureau, and also the curve of normal temperature for Cleveland It will be noted that the means for Cleveland follow closely the fluctuations recorded at North Chagrin. It is thus possible to construct a table of corrections for the Cleveland figures which may be used for further temperature studies at North Chagrin. Table 1 shows these corrections. It is apparent that the appearance of the leaves on the trees, and the development of a full and dense cover of foliage, which takes place from the middle of May to the middle of June is a definite factor in modifying temperatures in

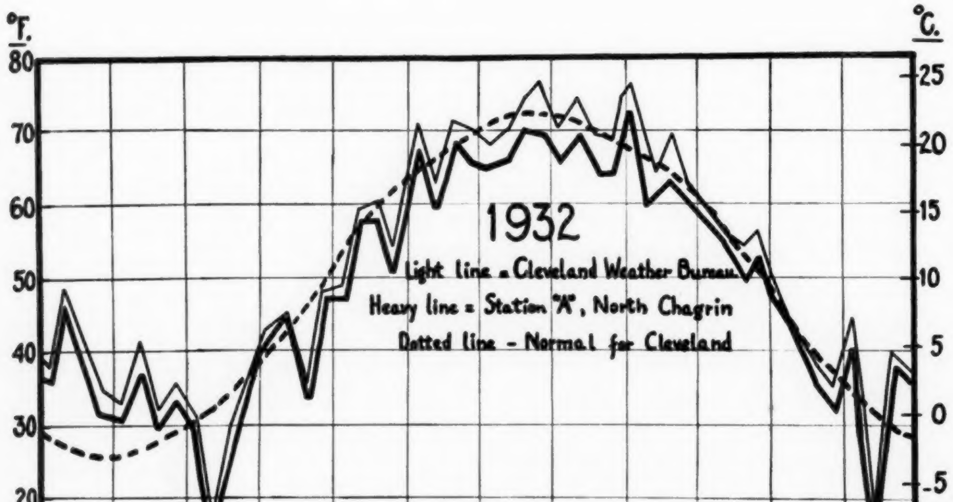

FIG. 2. Mean temperature by weeks on the basis of hourly readings at station "A," 1932, with mean temperature recorded for the same period by the Cleveland Weather Bureau. Curve of normal temperature for Cleveland.

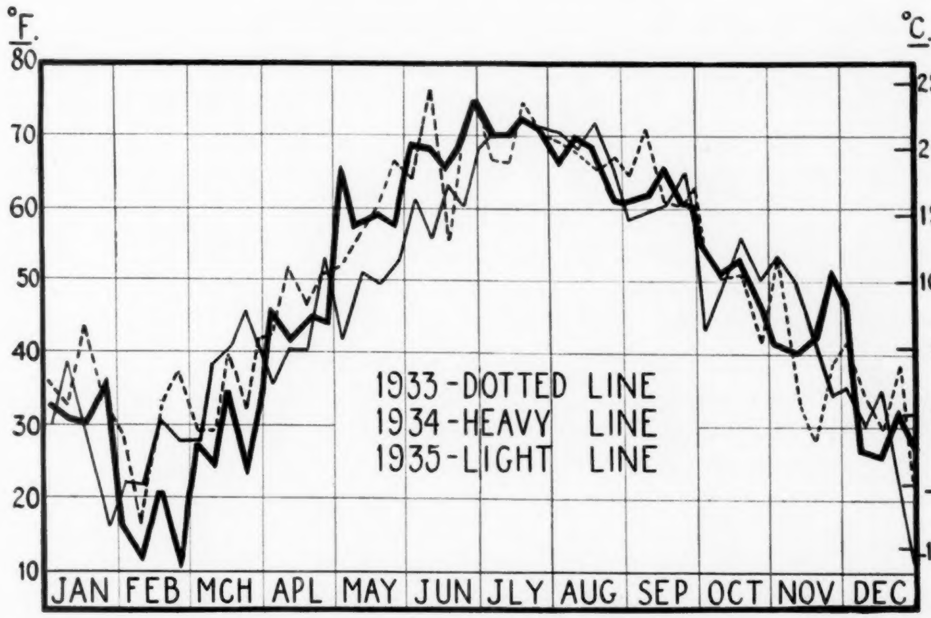

FIG. 3. Weekly mean temperature at North Chagrin, 1933, 1934, and 1935, from Cleveland Weather Bureau figures corrected in accordance with table 1.

the beech-maple forest. The Cleveland station of the U. S. Weather Bureau gives 200 days as the length of the growing season in this locality.

By the use of the correction figures (Table 1) the mean weekly temperatures at North Chagrin for the years 1933, 1934, and 1935 are shown not to be greatly different from those of 1932 (Fig. 3). Differences in temperatures recorded at the 4 stations were not great enough to be considered especially significant. After the middle of May when the leaves were on the trees there was little or no difference in the minima and but slight difference in

TABLE 1. Differences between temperatures at Cleveland and at North Chagrin, 1932, averaged for each month, and figures used for correcting Cleveland temperature records to show conditions at North Chagrin. (1° F. = 0.56° C.).

Month	Weekly Mean		Weekly Maximum		Weekly Minimum	
	Actual Difference	Correction Figure	Actual Difference	Correction Figure	Actual Difference	Correction Figure
January	—2°F.	—2°	—2°F.	—3°	—1°F.	—1°
February	—3	—2	—5	—3	—2	—1
March	—2	—2	—4	—3	—4	—4
April	—1	—2	0	—3	—3	—4
May	—2	—2	—1	—3	—4	—4
June	—4	—4	—3	—3	—6	—6
July	—5	—5	—5	—5	—4	—6
August	—5	—5	—6	—6	—6	—6
September	—4	—4	—6	—6	—9	—6
October	—3	—3	—4	—4	—3	—3
November	—2	—2	—3	—4	—3	—3
December	—2	—2	—4	—4	—1	—1

the maxima of all stations, 4° being the greatest divergence recorded. It may be said, then, that temperature in the area at five feet above the ground is practically uniform throughout, whether in beech-maple or in beech-hemlock environment, except as affected in minor ways by exposure or shelter.

Relative Humidity

Figure 4 shows the weekly means of the records of relative humidity on the basis of hourly readings at Station A for the year 1932. The mean relative humidity for the year was 83.3 per cent. When a comparison by weeks is made it appears that with few exceptions the amount of relative humidity was generally between 75 and 90 per cent. Records of many hours showed frequent periods of 100 per cent. A notable exception occurred during the latter part of April, a time of low precipitation, when great extremes of humidity were recorded daily, the record fluctuating between 16 and 100 per cent.

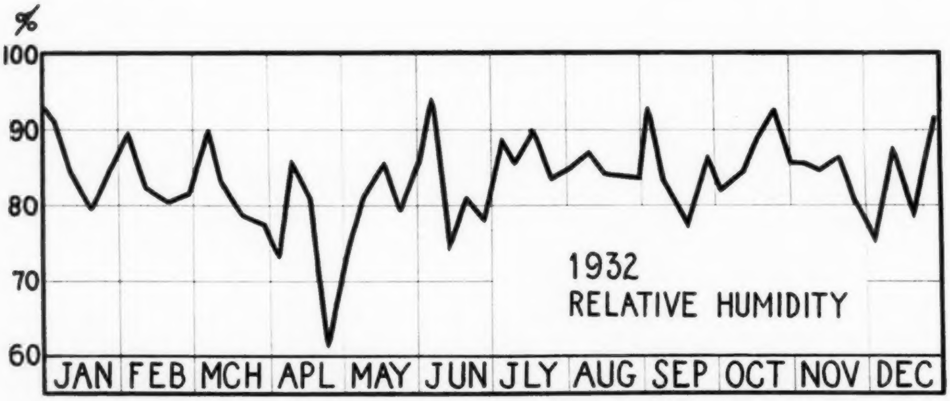

Fig. 4. Mean relative humidity by weeks on the basis of hourly readings station "A," 1932.

Precipitation

Records of amount of precipitation were obtained weekly during 1932 at all 4 stations. The individual instruments at times varied somewhat as to amount of water collected, but in the long run they approximated fairly closely (Table 2).

Table 2. Total precipitation at 4 stations: January 1 to December 31, 1932.

Station A	— beech-maple	— 31.70 inches	(80.52 cm.)
Station B	— beech-maple	— 32.41 inches	(83.32 cm.)
Station C	— beech-hemlock	— 29.23 inches	(74.24 cm.)
Station D	— beech-hemlock	— 29.11 inches	(73.94 cm.)

If the records of the two stations in beech-maple environment be averaged, and compared with the average of the two stations in beech-hemlock environment, it appears that the hemlocks received 2.88 inches (7.31 cm.) less water about their roots during the year than did the deciduous trees.

Since so little variation in precipitation was shown between the stations, the taking of further precipitation records was continued at Station B only. The records at this station by months for the 4 years of this study is shown in Figure 5, use being made of the diagrammatic method first introduced by Transeau in 1931 (Cain 1932). A study of these precipitation patterns discloses the fact that in 1932, during the growing season and immediately before, precipitation was very light, and that again in 1933 conditions during the growing season were marked by a deficiency of moisture. In fact, such rain as did fall in the summer of 1933 was concentrated in a few downpours which, because of the rapid run-off and speedy evaporation, was very ineffective, hardly reaching the soil beneath the forest litter to any great extent.

The year 1934, however, proved to be one in which precipitation, though deficient in May, was above normal in the summer and autumn, although this was the year of the great drought in other parts of the country. Because this record seems unusual it is fortunate that records of precipitation are available for the summer and early autumn of this year from the farm of Mr. B. P. Bole at Kirtland Hills, about 6 miles (9.65 kilometers) to the northeast, as a check upon the North Chagrin records. As a further check 2 additional rain gauges were operated in the spring of 1935 on either side of the North Chagrin instrument and about 10 feet (3 meters) away from it. Over a period of 4 weeks all three instruments were found to be in accord. For purposes of comparison the Bole farm records and those of the Cleveland Weather Bureau for 1934, as well as the normal precipitation for Cleveland, are included in Figure 5. As a matter of general observation it may be said that weather conditions at Cleveland and at North Chagrin are frequently not the same.

Wind

That the forest is responsible in many ways for its own micro-climate is strikingly shown in the way in which the movement of wind within its borders is modified by the presence of trees and other plants both in summer and in winter.

Toward the west the edge of the forest under study is bordered by an open field, and so presents an unbroken front to the full force of the wind from this direction. At this point, readings with an anemometer of the "windmill" type, measuring the velocity of the wind in feet, were taken over periods of 5 minutes each, first outside the forest, to measure the force of the wind at this point, and at each succeeding 100 feet (30.48 meters) within the forest, following the direction of the wind, until a point 1,000 feet (304.8 meters) from the edge was reached. The velocity of the wind at the outside was then again measured, and the average of this, and the first outside measurement taken as the velocity of the wind during the hour or more consumed in taking all of the records. Six such

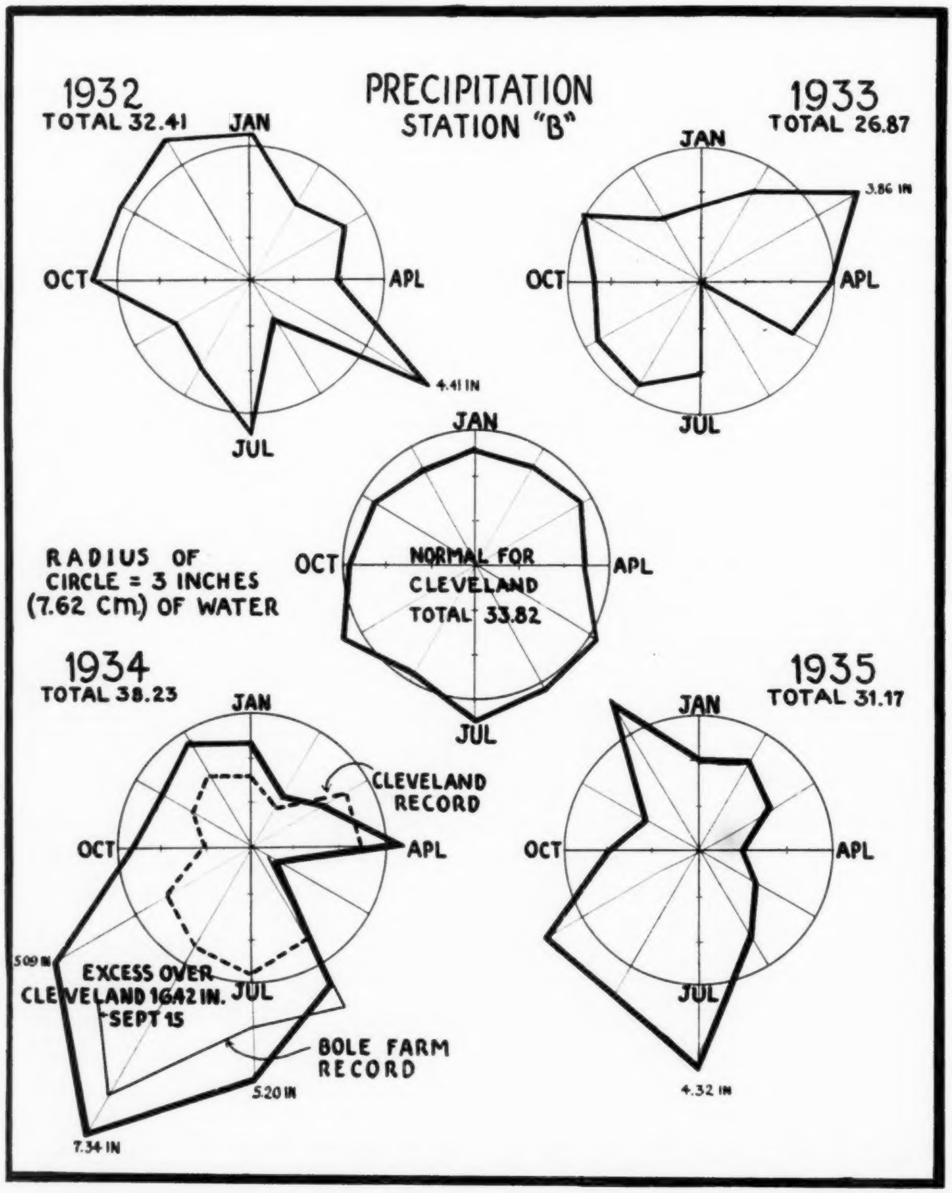

FIG. 5. Precipitation by months, station "B," 1932, 1933, 1934, and 1935, with Bole Farm records and Cleveland records for 1934, and normal for Cleveland.

complete records were obtained at various times and under various conditions when the trees were bare of foliage, and five complete records when the trees were in full leaf. Table 3 shows the amount of decrease in velocity after reaching the 800-foot mark. Records are reduced to feet per minute.

Reduced to percentages of decreased velocity from the forest edge inward, the results of these records are given in Figure 6. The records from the 700-foot point and further were usually of light and shifting air cur-

TABLE 3. Effect of forest on wind velocity.
(records in feet per minute)

Trees Without Leaves			Trees With Leaves		
Record	Average velocity in open	Average velocity 800-1000 ft.	Record	Average velocity in open	Average velocity 800-1000 ft.
1.	862 f.p.m.	161 f.p.m.	1.	763 f.p.m.	47 f.p.m.
2.	826	168	2.	573	22
3.	671	111	3.	481	27
4.	615	172	4.	343	23
5.	495	175	5.	284	64
6.	339	159			

NOTE: 100 feet = 30.48 meters.

rents. Several readings taken further within the forest showed essentially the same conditions. Comparing summer and winter conditions it appears that there is from 13 to 20 per cent more air in motion near the ground in winter than in summer.

SUNSHINE

Figure 7 shows the possible number of hours of sunshine by months for Cleveland, and also the actual number of hours of sunshine for the year 1932. For purposes of comparison the curve of the normal number of hours of sunshine for Cleveland is included. It is apparent that the total amount of cloudiness during the year is very considerable. Even though there were actually more hours of sunshine than normal in 1932 for 8 months out of 12, the actual number of hours of sunshine for the year were only 56 per cent of the possible number—the normal being 52 per cent. During the winter months, December, January, and February, the normal proportion of sunshine sinks to 24, 29, and 35 per cent of the possible number of hours.

While no measurements of light intensities were made, it should be noted that the beech-maple-hemlock forest is a dark forest in summer. One of the first things of which one becomes conscious upon entering this forest on a bright summer day, is of the great decrease of light intensity. The eyes need to become adjusted to this condition before much can be seen. The writer has frequently made exposures of 15 seconds duration on photographic film in order to get good pictures within the forest on days when the summer sun was shining brightly outside. Using the same aperture, lens, and film in the open on such a day would have necessitated an exposure of one-fiftieth of a second. Although this is by no means an exact measurement, it does indicate that light within the forest is one-seven-hundred-and-fiftieth as effective on photographic film in midsummer as it is outside the forest at the same time and otherwise under the same conditions.

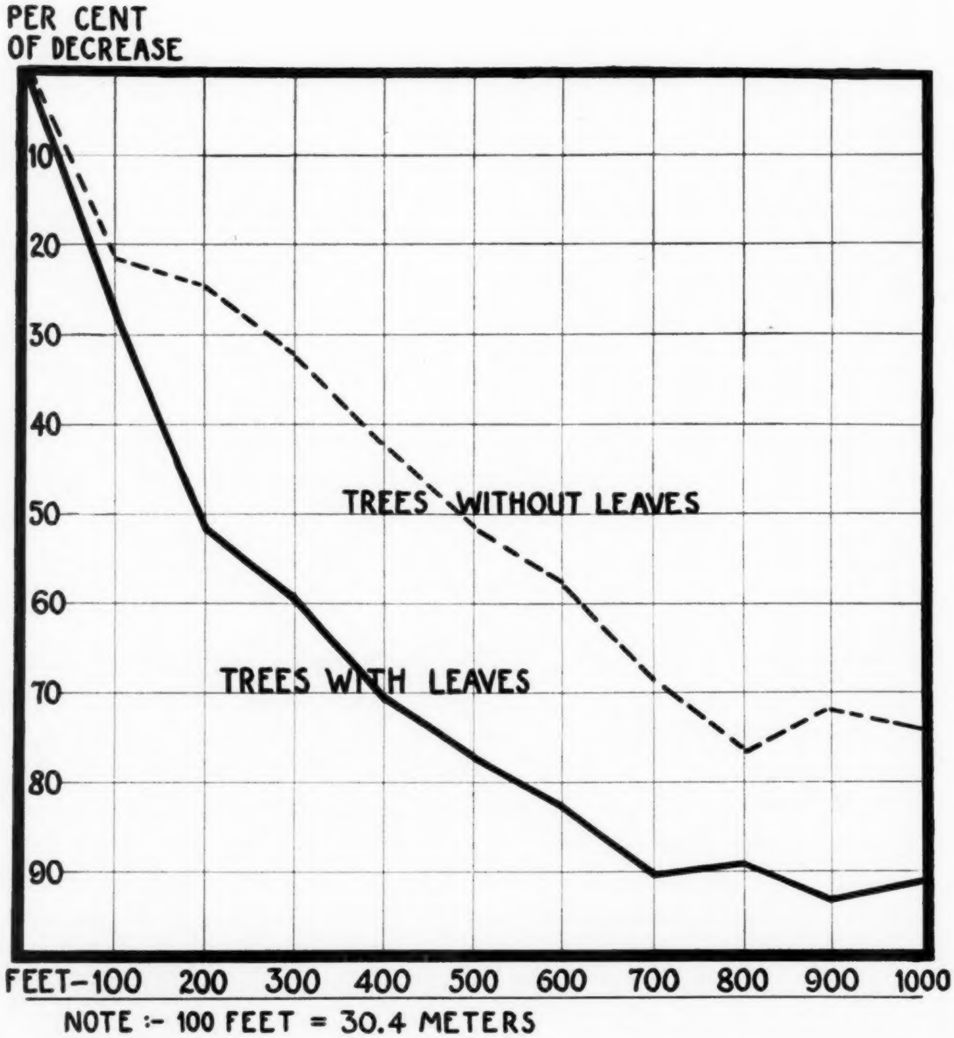

FIG. 6. Decrease in velocity of wind from forest edge inward in summer (heavy line) and winter (dotted line).

EVAPORATION RATE

During the summer of 1934 an attempt was made to secure data on the rate of evaporation of moisture, both in the forest, and in the open just outside the woods to the west. For this purpose standardized Livingston porous clay bulb atmometers were used, evaporating distilled water only. Although a group of three instruments were run in the woods, so that readings might be averaged, continual interference with the bulbs by gray squirrels, and the growth of protococcus on the bulbs at times, reduced the number of available instruments often to two, and sometimes to one. There were also two short periods when all instruments in the woods were out of

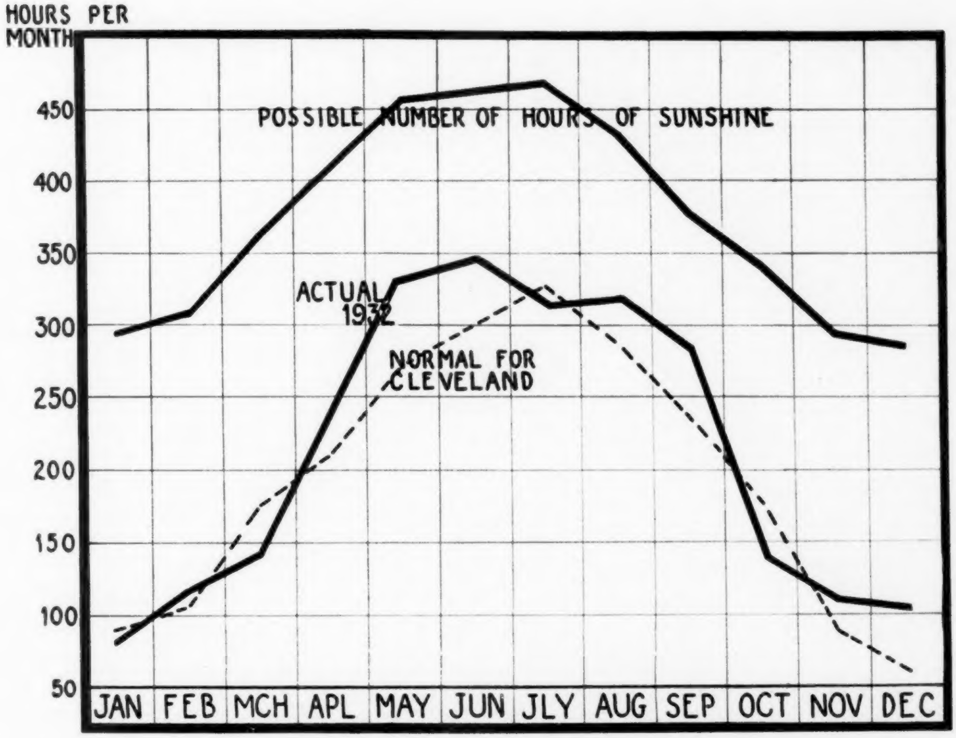

FIG. 7. Possible and actual number of hours of sunshine for Cleveland in 1932, and normal for Cleveland.

commission due to these causes. The one instrument in the open field ran continuously without interruption from August 1 to October 15 when the bulb was shattered by freezing. To get some idea of winter conditions, readings were taken twice over short periods in November and January when the temperature was above freezing. Table 4 gives the data obtained from these instruments.

The rate of evaporation is apparently affected greatly by various atmospheric conditions. Wind greatly increases it. Precipitation in summer and freezing in winter slows it up. High temperature with dryness is conducive to a high evaporation rate. The effect of the forest in reducing the rate of evaporation within its borders, as compared with conditions in the open, is striking, showing an average difference of 55.2 per cent in summer when the leaves are on the trees, and of 38 per cent in winter when the forest is more exposed to the influence of wind.

SUMMARY OF CLIMATIC DATA

From the data gathered over the four-year period of this study, the climate of the area may be summarized by saying that temperatures are not extreme, varying from -13° F. (-25° C.) in winter to 96° F (35.5° C.)

TABLE 4. Evaporation rates at approximately 12 inches (0.304 m.) above ground.

Date—*1934*		Open field. Rate of evaporation in cc. per hour	Beech-maple. Rate of evaporation in cc. per hour	Per cent of decrease from open to forest	Weather conditions
June	1 - 4..	.....	0.835	....	very dry
	4 - 11..	.....	0.713	....	very dry
	11 - 25..	.....	0.524	....	wet
	25 - 2..	.....	0.402	....	very wet
July	2 - 9..	.....	0.404	....	very wet
	9 - 16..	.....	0.271	....	very wet
August	1 - 6..	0.940	0.350	62.8	very wet
	6 - 13..	0.807	0.285	64.7	very wet
	13 - 22..	0.740	No record	....	very wet
	22 - 27..	0.760	0.270	64.5	very wet
	27 - 1..	0.610	0.255	58.2	wet
September	1 - 10..	0.497	0.275	44.7	wet
	10 - 17..	0.287	0.152	47.1	wet
	17 - 24..	0.520	0.231	35.6	wet
	24 - 1..	0.428	0.223	47.9	wet
October	1 - 8..	0.619	0.180	71.0	very wet
	8 - 15..	0.481	0.307	36.2 (leaves falling)	—dry
November	24 - 26..	1.137	0.757	33.5 (heavy wind)	—dry
1935					
January	6 - 7..	0.402	0.231	42.6 (ground frozen)	

Average evaporation in forest, June 1 to October 15, — 0.355 cc. per hour per instrument.

in summer; that it may be subject to unseasonable weather, but that for the most part temperatures are within closer limits; that relative humidity is high, for most of the time ranging between 75 and 90 per cent; that precipitation is rather uniform throughout the year, averaging 2.84 inches (7.21 cm.) per month, or 31.62 inches (80.31 cm.) per year for the period of this study; that for 52 per cent of the time when sunshine is possible the sky is overcast; that the force of the wind is ordinarily so tempered by the trunks and branches of the trees in winter, and the addition of their foliage mass in summer, as to make wind disturbances rare throughout its lower levels; that the rate of evaporation is reduced within the forest from 47.1 to 64.7 per cent in summer to from 33 to 42.6 per cent in winter, as compared with the open field at its western edge.

HISTORY OF THE AREA STUDIED

The former Indian occupation of this region is well attested by the collections of flint and stone implements assembled over a period of years by Mr. Ray Parker and Mr. Carl Scheuring whose farms are located close to the area on the southwest. The forest of the area, says Mr. A. C. Keesler, who has lived all his life nearby, has always been a beech woods. The large stumps, well advanced in decay, seen occasionally in the woods, he says represent a cutting made when he was a boy of about 14 (1871), when some large oak, hickory and tulip trees were taken out for lumber. Ap-

parently the particular portion of the area in which our interest centers has suffered little from major disturbances for a long time. There is no evidence of serious fire, either in the place itself, or in the memories of those who, like Mr. Keesler, have a long family tradition associated with the place.

In 1925, 1926, and 1927, the Cleveland Metropolitan Park Board acquired practically all of the 1,201 acres (486.04 hectares) now known as the North Chagrin Reservation, and containing the area under study. Since that time all wild life within the boundaries of the reservation, including both plants and animals, has been under complete protection, no hunting, or other disturbance of natural conditions having been allowed. The policy of the Park Board has been that of conserving natural conditions as far as possible. Picnic grounds and playgrounds are located outside the forested areas. Foot-trails give access to the forest, but there has as yet been little straying from the trails on the part of visitors. No picnic parties are allowed within the woods. One bridle-path crosses the area, and another skirts its western edge. Two uniformed guards regularly patrol the entire reservation to see that park regulations are respected.

CHARACTER OF THE FOREST

Plant Constitution

TREES

In 1932 the writer had recourse to the familiar quadrat method of determining the abundance and distribution of trees and shrubs throughout the area, but as increasing familiarity with the forest was gained it became apparent that the results obtained by the quadrat method were far from satisfactory, and this method was abandoned. Instead, during the winters of 1933-34 and 1934-35, all of the larger trees of the area were measured, and their approximate location charted on individual maps for each species. Measurements were made by tape giving the circumference breast high in inches, and only trees of 30 inches (76.2 cm.) or over in circumference, or slightly over 9.5 inches (24.13 cm.) in diameter, were thus measured and their location charted. Later, a count of all trees of each species was made, section by section, but without the use of quadrats or other measured areas. In this count an effort was made to include all trees down to the 3.5 inch (8.9 cm.) diameter class, the size being judged by eye. While the figures thus obtained are doubtless subject to some error the writer believes them to be substantially in accord with the facts.

On the basis of these counts and maps (Figs. 9 and 10) it appears that there exist 4 major vegetational divisions within the area (Fig. 8) which may be designated as follows:

(1) *The spurs of the eastern edge of the area.* Here occurs a forest mictium including beech, hemlock, red oak, and chestnut, as dominants, together with a relatively large proportion of other species. Chestnut is assigned its position on the basis of large standing trees, though at the present time none are living. It was so recently an important member of this com-

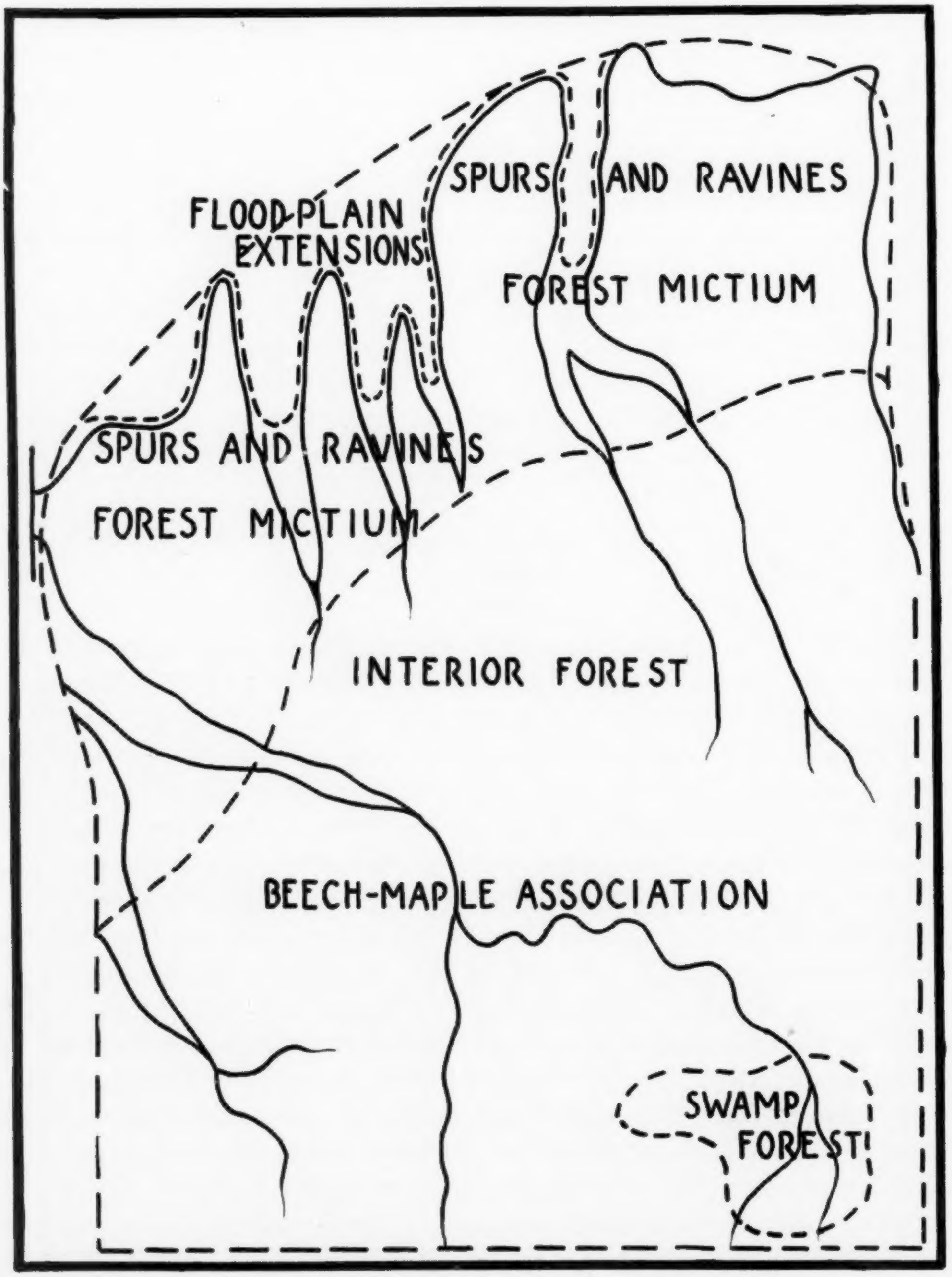

FIG. 8. Major vegetational divisions of the area under study.

munity that it seems desirable here and elsewhere in this study to recognize its former significance.

(2) *The ravines between the spurs.* In the deeper ravines an excess of moisture is always present. Here herbaceous vegetation prolongs its sea-

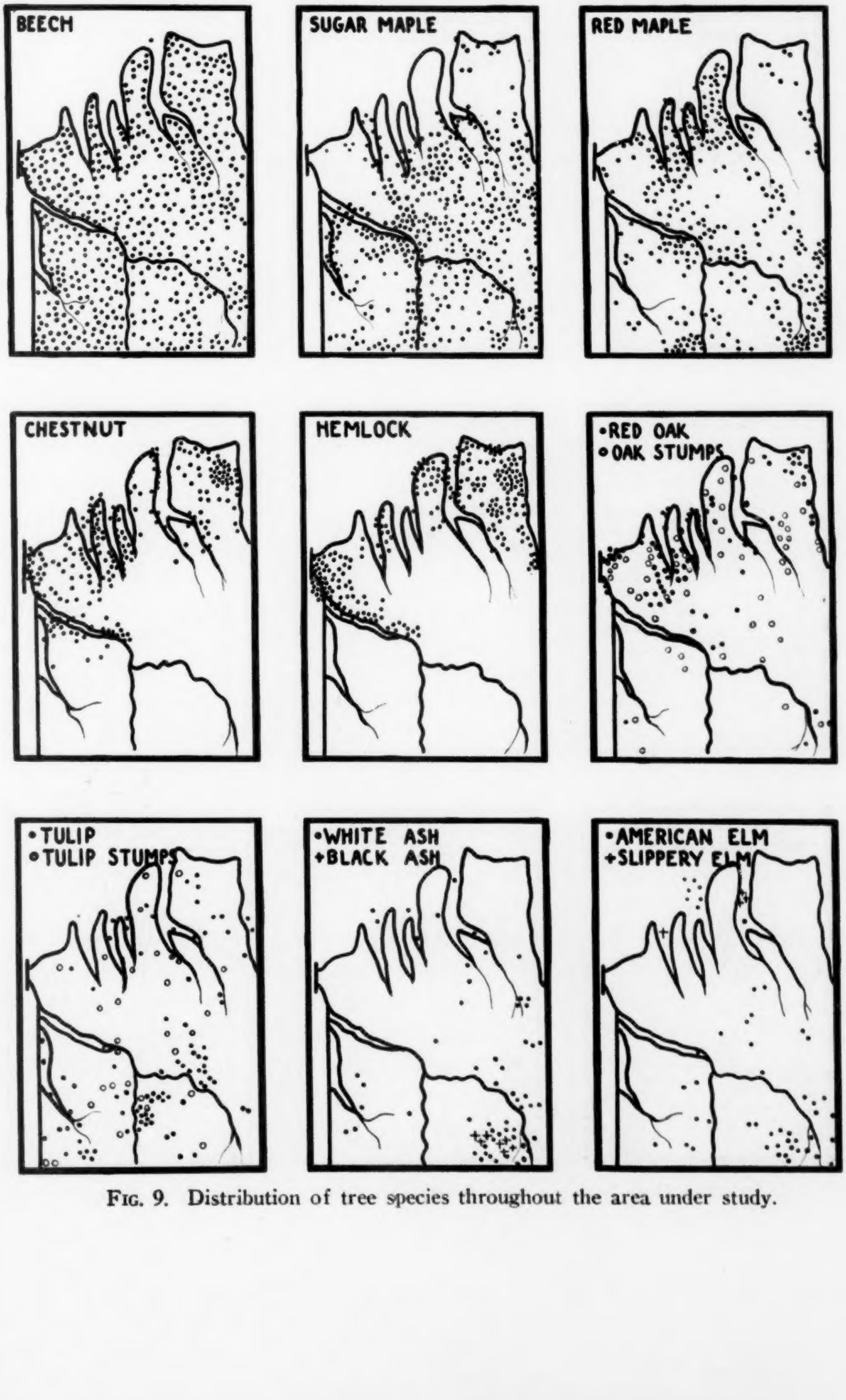

FIG. 9. Distribution of tree species throughout the area under study.

son and grows to larger size than upon the upland. Only here can ferns be said to be well developed. Trees in the ravines often represent bottomland species which have thus extended the flood-plain forest into the area, bringing in some species which otherwise seem out of place. Beech is

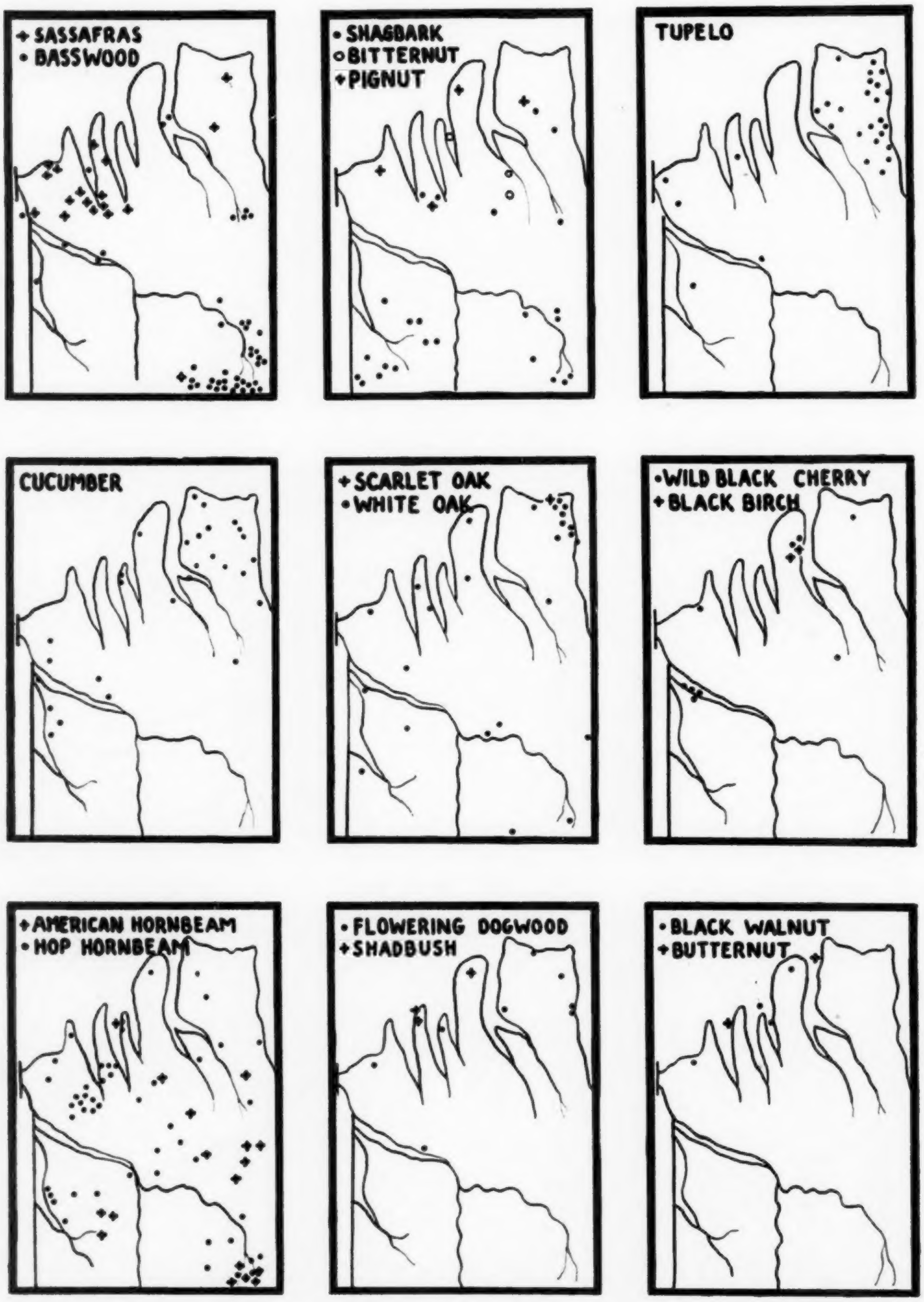

FIG. 10. Distribution of tree species throughout the area under study.

absent from the ravines but sugar maple and tulip are present, and in certain places hemlock is found in the ravines. Thus the ravines might be considered as the beginning of a transition stage toward swamp forest or flood-plain conditions.

(3) *The western forest edge, and particularly its southwest corner.* Here, with the exception of some large American elms, the forest is younger than elsewhere, and its character leads one to believe that a portion of it may have served at one time as a "wood-lot" in which only the elms were left undisturbed. The southwest corner has considerable standing water in it during most of the year which accounts for the numbers of American elm, basswood, and red maple here, and the presence of black ash; suggesting the elm-black ash-red maple association described by Sampson (1930) as characteristic of the swamp forest of northeastern Ohio.

(4) *The interior forest.* This includes the larger part of the area under study. The land here is relatively level, and the forest is quite uniformly beech and sugar maple in varying proportions, including a few other associated species as secondary or incidental dominants.

Table 5 shows the abundance and distribution of tree species throughout the four habitats above described. Figure 11, following the method used by Sampson (1930), reduces Table 5 to graphic form. Scientific names in this, and in the following lists of vascular plants, are as given in Gray's Manual of Botany, seventh edition (1908).

Taking the forest as a whole it should be noted that beech composes 51 per cent of it, sugar maple 26.5, red maple 7.2, and hemlock 6.6 per cent. These four species together thus make up 91.4 per cent of the forest. Inasmuch as chestnut has already ceased to be a factor in the community, and, as will be shown later, hemlock and red oak are tending toward exclusion, and tulip and white ash are here secondary succession trees, it appears that the species of greatest importance in this forest are beech, sugar maple, and red maple.

SUBDOMINANT GREEN PLANTS

In this group belong the shrubs, the herbs, the ferns, the climbers, twiners and trailers, and other low-growing plants. As the shrub layer society is very poorly and irregularly developed throughout the entire area, significant differences in the distribution of the plants of this list (Table 6) are largely as between beech-maple and beech-hemlock environments, and their occurrence in either or both of these associations is noted. The order of listing, except in the case of the uncommon to rare species, or unless otherwise noted, is in the order of their abundance.

Spicebush is the most abundant shrub in the area, but it is concentrated largely in two rather moist situations. Maple-leaved viburnum is better distributed than spicebush, but occurs only sparingly. Red-berried elder is

TABLE 5. Species, abundance, and distribution of trees of 3.5 inches in diameter and over.

Species	Beech-maple association		Beech-hemlock-oak-chestnut mictium		Transition toward swamp forest: In ravines		Transition toward swamp forest: Swampy area			
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	Totals	Per cent
Beech—*Fagus grandifolia* Ehrh.	1920	52.6	707	43.0	....	....	87	28.4	2714	47.2
Sugar Maple—*Acer saccharum* Marsh.	1193	32.7	124	7.5	19	13.0	79	25.6	1415	24.6
Red Maple—*Acer rubrum* L.	227	6.2	113	7.0	10	7.0	31	10.0	381	6.6
Hemlock—*Tsuga canadensis* (L.) Carr.	36	1.0	242	14.9	72	49.0	....	....	350	6.1
Chestnut—*Castanea dentata* (Marsh.) Borkh.	36	1.0	235	14.9	....	....	....	....	271	4.7
Tulip—*Liriodendron tulipifera* L.	110	3.0	14	0.9	6	4.0	2	0.7	132	2.3
Red Oak—*Quercus rubra* L.	8	0.2	78	4.8	5	3.4	3	1.0	94	1.6
White Ash—*Fraxinus americana* L.	25	0.7	....	....	7	4.7	29	9.5	61	1.1
American Elm—*Ulmus americana* L.	18	0.5	....	....	7	4.7	24	8.0	49	0.9
Hop Hornbeam—*Ostrya virginiana* (Mill.) K. Koch	18	0.5	21	1.2	....	....	6	2.0	45	0.8
Basswood—*Tilia americana* L.	7	0.2	....	....	6	4.0	25	8.2	38	0.7
Shagbark Hickory—*Carya ovata* (Mill.) K. Koch.	20	0.5	4	0.2	....	....	7	2.3	31	0.6
Tupelo—*Nyssa sylvatica* Marsh.	5	0.1	21	1.2	....	....	....	....	26	0.4
Cucumber—*Magnolia acuminata* L.	7	0.2	18	1.1	....	....	....	....	25	0.4
White Oak—*Quercus alba* L.	7	0.2	16	0.9	....	....	1	0.3	24	0.4
Sassafras—*Sassafras varriifolium* (Salisb.) Ktze.	3	0.1	15	0.9	....	....	....	....	18	0.3
American Hornbeam—*Carpinus caroliniana* Walt.	11	0.3	1	0.0	....	....	6	2.0	18	0.3
Flowering Dogwood—*Cornus florida* L.	1	0.0	10	0.6	....	....	....	....	11	0.2
Wild Black Cherry—*Prunus serotina* Ehrh.	1	0.0	5	0.2	3	2.0	....	....	9	0.2
Slippery Elm—*Ulmus fulva* Michx.	....	....	....	....	6	4.0	....	....	6	0.1
Black Ash—*Fraxinus nigra* Marsh.	....	....	....	....	....	....	6	2.0	6	0.1
Black Walnut—*Juglans nigra* L.	....	....	2	0.1	2	1.4	....	....	4	0.1
Pignut—*Carya glabra* (Mill.) Spach.	....	....	4	0.2	....	....	....	....	4	0.1
Bitternut—*Carya cordiformis* (Wang.) K. Koch.	1	0.0	....	....	2	1.4	....	....	3	
Shadbush—*Amelanchier canadensis* (L.) Medic.	....	....	3	0.2	....	....	....	....	3	
Butternut—*Juglans cinerea* L.	....	....	....	....	2	1.4	....	....	2	0.2
Black Birch—*Betula lenta* L.	....	....	2	0.1	....	....	....	....	2	
Scarlet Oak—*Quercus coccinea* Muench.	....	....	1	0.0	....	....	....	....	1	
Totals	3654	....	1638	....	147	....	306	....	5745	100.0

commonly found as a subseral plant where the soil has been disturbed. In most cases the shrubs give the impression of struggling under severe limitations. Their development is usually poor, and they fruit sparingly except in open situations.

In the beech-maple association the herbaceous plants grow luxuriantly, and produce annually a tremendous crop of seeds, fruits, and other food reserves stored in corms, tubers, root-stocks, and other like structures. Spring beauty, spring cress, cut-leaved dentaria, and yellow adder's tongue occur in great numbers on the higher land where there is usually a surplus of standing water in April and May. In certain places the forest floor may aptly be said to be "carpeted" with the blooms of these species. The two trilliums are very abundant in the mid-portion of the area, and grow to large size in the ravines. Dutchman's breeches is common on the higher ground, while squirrel corn seems to prefer the sides of the ravines. Four

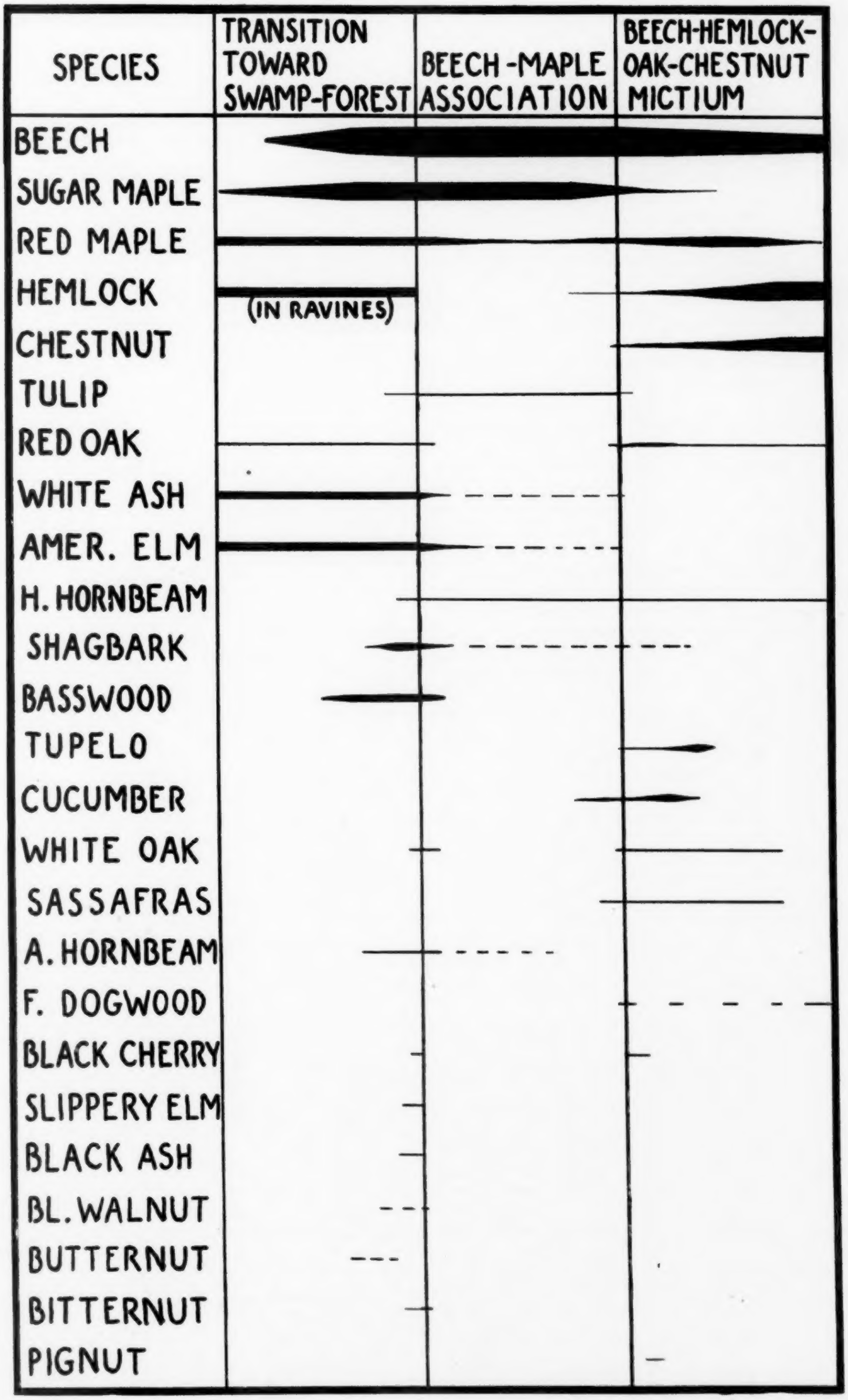

FIG. 11. Distribution and abundance of tree species showing relation to beech-maple association and contiguous forest types.

TABLE 6. Subdominant green plants.

	Beech-maple	Beech-hemlock
1. SHRUBS:		
Spicebush—*Benzoin aestivale* (L.) Nees	*	
Maple-leaved Viburnum—*Viburnum acerifolium* L.	*	*
Red-berried Elder—*Sambucus racemosa* L.	*	
Highbush Blackberry—*Rubus allegheniensis* Porter	*	
Prickly Gooseberry—*Ribes cynosbati* L.	*	*
Purple-flowering Raspberry—*Rubus odoratus* L.	*	
Witch Hazel—*Hamamelis virginiana* L.	*	*
Choke Cherry—*Prunus virginiana* L.	*	
Common Elder—*Sambucus canadensis* L.	*	
Fly Honeysuckle—*Lonicera canadensis* Marsh		*
Bush Honeysuckle—*Diervilla lonicera* Mill.		*
Low Sweet Blueberry—*Vaccinium pennsylvanicum* Lam.		*
Leatherwood—*Dirca palustris* L.		*
2. CLIMBERS, TWINERS, AND TRAILERS:		
Northern Fox Grape—*Vitis labrusca* L.	*	
Trailing Euonymus—*Evonymus obovatus* Nutt.	*	
Virginia Creeper—*Psedera quinquefolia* (L.) Greene	*	*
Poison Ivy—*Rhus toxicodendron* L.	*	
Green Brier—*Smilax rotundifolia* L.	*	
Carrion Flower—*Smilax herbacea* L.	*	
Bittersweet—*Celastrus scandens* L.	*	
3. HERBS AND LOW SHRUBBY PLANTS:		
a. Abundant species (somewhat in the order of their flowering)		
Hepatica—*Hepatica acutiloba* DC	*	
Spring Beauty—*Claytonia virginica* L.	*	
Yellow Adder's Tongue—*Erythronium americanum* Ker.	*	
Round-leaved Violet—*Viola rotundifolia* Michx.	*	
Halberd-leaved Violet—*Viola hastata* Michx.	*	
Wake Robin—*Trillium erectum* L.	*	
Dutchman's Breeches—*Dicentra cucullaria* (L.) Bernh.	*	
Cut-leaved Dentaria—*Dentaria laciniata* Muhl.	*	
Spring Cross—*Cardamine bulbosa* (Schreb.) BSP	*	
Squirrel Corn—*Dicentra canadensis* (Goldie) Walp.	*	
Rue Anemone—*Anemonella thalictroides* (L.) Spach.	*	
Great White Trillium—*Trillium grandiflorum* (Michx.) Salisb.	*	
Wild Ginger—*Asarum canadense* L.	*	
Sweet Cicely—*Osmorhiza claytoni* (Michx.) Clarke	*	
Toothwort—*Dentaria diphylla* Michx.	*	
Oakesia—*Oakesia sessilifolia* (L.) Wats.	*	
Downy Yellow Violet—*Viola pubescens* Ait.	*	
Smooth Yellow Violet—*Viola scabriuscula* Schwein.	*	
Canada Violet—*Viola canadensis* L.	*	
Dwarf Ginseng—*Panax trifolium* L.	*	
Foam Flower—*Tiarella cordifolia* L.	*	
Solomon's Seal—*Polygonatum biflorum* (Walt.) Ell.	*	
Canada Mayflower—*Maianthemum canadense* Desf.		*
Jack-in-the-Pulpit—*Arisaema triphyllum* (L.) Schott.	*	
May Apple—*Podophyllum peltatum* L.	*	
False Spikenard—*Smilicina racemosa* (L.) Desf.	*	
Pale Jewelweed—*Impatiens pallida* Nutt.	*	
Spotted Jewelweed—*Impatiens biflora* Walt.	*	
Pokeweed—*Phytolacca decandra* L.	*	
b. COMMON SPECIES:		
Blue Cohosh—*Caulophyllum thalictroides* (L.) Michx.	*	
Large-flowered Bellwort—*Uvularia grandiflora* Sm.	*	
Swamp Buttercup—*Ranunculus septentrionalis* Poir.	*	

TABLE 6. Continued

	Beech-maple	Beech-hemlock
Yellow Rocket—*Barbarea vulgaris* R. Br.	*	
Common Violet—*Viola papilionacea* Pursh	*	
Indian Cucumber—*Medeola virginiana* L.	*	*
Wild Sarsaparilla—*Aralia nudicaulis* L.	*	
Twisted Stalk—*Streptopus amplexifolius* (L.) DC.	*	
Partridgeberry—*Mitchella repens* L.		*
White Baneberry—*Actaea alba* (L.) Mill.	*	
Wild Blue Phlox—*Phlox divaricata* L.	*	
Wild Geranium—*Geranium maculatum* L.	*	
Northern Bedstraw—*Galium boreale* L.	*	
Black Snakeroot—*Cimicifuga racemosa* (L.) Nutt.	*	
Wintergreen—*Gaultheria procumbens* L.		*
Richweed—*Pilea pumila* (L.) Gray	*	
c. UNCOMMON TO RARE SPECIES:		
Harbinger of Spring—*Erigenia bulbosa* (Michx.) Nutt.	*	
Bloodroot—*Sanguinaria canadensis* L.	*	
Trailing Arbutus—*Epigaea repens* L.		*
Perfoliate Bellwort—*Uvularia perfoliata* L.	*	
Early Meadow Rue—*Thalictrum dioicum*	*	
Wood Anemone—*Anemone quinquefolia* L.	*	
Wood Betony—*Pedicularis canadensis* L.	*	
Sweet White Violet—*Viola blanda* Willd.	*	
Great-spurred Violet—*Viola rostrata* Pursh	*	
Wood Sorrel—*Oxalis corniculata* L.	*	
Bishop's Cap—*Mitella diphylla* L.	*	
Golden Seal—*Hydrastis canadensis* L.	*	
Virginia Waterleaf—*Hydrophyllum virginianum* L.	*	
Pink Lady's Slipper—*Cypropedium acaule* Ait.		*
Agrimony—*Agrimoria striata* Michx.	*	
Monkey Flower—*Mimulus ringens* L.	*	
Round-leaved Orchid—*Habenaria orbiculata* (Pursh.)	*	
Great Lobelia—*Lobelia siphilitica* L.	*	
Wild Leek—*Allium tricoccum* Ait.	*	
Ginseng—*Panax quinquefolium* L.	*	
Indian Tobacco—*Lobelia inflata* L.	*	
Cardinal Flower—*Lobelia cardinalis* L.	*	
Nodding Pogonia—*Pogonia trianthophora* (Sw.) BSP	*	
Spikenard—*Aralia racemosa* L.	*	
4. FERNS:		
Christmas Fern—*Polystichum acrostichoides* (Michx.) Schot.	*	*
Spinulose Wood Fern—*Asplenium spinulosum intermedium* D. C. Eaton	*	*
Silvery Spleenwort—*Asplenium acrostichoides* Sw.	*	
New York Fern—*Aspidium noveboracense* (L.) Sw.	*	*
Marginal Shield Fern—*Aspidium marginale* (L.) Sw.	*	*
Rattlesnake Fern—*Botrychium virginianum* (L.) Sw.	*	
Broad Beech Fern—*Phegopteris haxagonoptera* (Michx) Fee	*	
Maidenhair Fern—*Adiantum pedatum* L.	*	*
Long Beech Fern—*Phegopteris polypodioides* Fee.	*	
Sensitive Fern—*Onoclea sensibilis* L.	*	
Ternate Grape Fern—*Botrychium ternatum intermedium* D. C. Eaton	*	
Interrupted Fern—*Osmunda claytoniana* L.	*	
Narrow-leaved Spleenwort—*Asplenium angustifolium* Michx.	*	(in ravines)
Hay-scented Fern—*Dicksonia punctilobula* (Michx.) Gray	*	

TABLE 6. Continued

	Beech-maple	Beech-hemlock
5. MOSSES:		
Amblystegium serpens (L.) B & S	*	*
Thuidium delicatulum (L.) Mitt.	*	
Hypnum haldanianum Grev.	*	
Hypnum reptile Mx.	*	
Funaria hygrometricia (L.) Sibth.	*	
Leucobryum glaucum (L.) Schimp.		*
Mnium cuspidatum (L.) Leyss.	*	*
Dicranella heteronalla (L.) Schimp.	*	*
Catharinea undulata (L.) W & M	*	
Fissidens taxifolius (L.) Hedw.	*	
6. MISCELLANEOUS:		
Sedge—*Carex plantaginea* Lam.	*	
Club Moss—*Lycopodium lucidulum* Michx.		*
Lichen—*Cladonia fimbriata* (L.) Hoffm. Deutsch.	*	*
Liverwort—*Marchantia polymorpha* (L.)	*	
Alga—*Microspora amoena* (Kütz.) Lagerh.	*	
Alga—*Protococcus* sp. (on beech trunks)	*	*

species of yellow violets bloom abundantly. Hepatica grows in masses in moist places along the water-courses and on the edges of the ravines. False spikenard, solomon's seal, and twisted stalk are quite generally distributed. Wild ginger and May apple cover the ground with their characteristic leaves in certain locations. Jack-in-the-pulpit and blue cohosh are well distributed. The tiny dwarf ginseng, in its season, shows its small puff-balls of white bloom throughout the forest. The evergreen leaves of foam flower are common in the wetter places, and over the edges of the ravines. Those curious plants, beech drops, and squaw root, are common, the former more so than the latter; and the pale Indian pipe is found frequently. The late-comers, white baneberry and black snake-root, are common. Jewelweed and pokeweed grow luxuriantly in certain places.

In great contrast to this rich development of herbaceous growth beneath the beeches and maples is the thinly spread ground cover beneath the hemlocks. The common herbaceous plant of the beech-hemlock association is the Canada mayflower. In certain locations it covers the ground, but it is the only plant of which this can be said. In this environment partridge berry and wintergreen appear frequently. Apart from these there is very little. It is in this habitat that a few plants of pink lady's slipper and trailing arbutus occur.

This difference in herbaceous growth was studied in Indiana by Daubenmire (1930), who concluded that, of the factors studied (light, evaporation rate, soil acidity, soil moisture), soil moisture conditions exerted the most inhibitive influence on vegetational development under hemlock, while the

greater acidity of the surface soil is probably a contributing factor in the inhibition of forest floor herbs.

In no place in the area do ferns grow in abundance. Small societies of New York fern occur sparingly on the higher land and on some of the spurs. Christmas fern, marginal shield fern, and spinulose wood fern are all well distributed as individual plants, reaching their best development along the edges of the gullies and ravines. Rattlesnake fern is well distributed on the higher land. Other ferns on the list occur only occasionally. In general, while most of these ferns may be found in both associations, they are more abundant in beech-maple than in beech-hemlock environment, and are best developed in the ravines and along their sides. There is little poison ivy in the area, and such as there is, is confined to the beech-maple association on higher ground. In places Virginia creeper grows as ground cover, and in a few places it ascends the trees. In certain locations in the beech-maple association trailing euonymus forms dense mats as ground cover.

The vine *par excellence* in the area is the northern fox grape. It may form tangles in the tops of large standing trees, or hang in a dense "curtain" from lofty supports, or create tangles on the ground when the original supporting trees have broken down, letting the whole mass down to ground level. In the latter case a great opening is made in the forest canopy. Secondary succession after grapes is obscure, as nothing grows beneath the grapes in this condition.

Neither mosses nor lichens are particularly abundant in the area. Probably the creeping hypnum, *Amblystegium serpens*, growing on logs and stones, is the most common moss in the beech-maple association, and the cushion moss, *Leucobryum glaucum*, is the most common in the beech-hemlock association. The sedge, *Carex plantaginea*, is one of the well distributed plants of the beech-maple association.

SAPROPHYTES AND PARASITES

Saprophytic and parasitic plants in the area fall in two main groups—flowering plants and fungi. They are listed in Table 7. Although the fungi listed represent four seasons of observation it is realized that the list is far from complete, as new species are constantly being added. However, it may be assumed that those species that are of greatest importance in the area, because of their abundance, regularity of appearance, or wide distribution, are noted herein.

Doubtless because of the long time during which the natural processes of decay have been at work in the forest under study, the number of species, and the abundance of certain fungi, is great. In fact, Mr. Henry C. Beardslee, an authority on Ohio fungi, gives it as his opinion that from 1,200 to

TABLE 7. Saprophytic and parasitic plants.

1. Flowering plants.
   Beech Drops—*Epifagus virginiana* (L.) Bart. (beech-maple association)
   Squaw Root—*Conopholis americana* (L.f.) Wallr. (beech-hemlock association)
   Indian Pipe—*Monotropa uniflora* L. (beech-maple association)
2. Fungi.
   A. Abundant fungi (in order of abundance)
      a. Woody brackets
         Polyporus applanatus Fr.
         Polyporus resinosus (Fr.) Schrader.
         Polyporus gilvus (Fr.) Schw.
      b. Leathery brackets
         Polyporus versicolor Fr.
         Polystictus pergamenus Fr.
         Stereum spadiceum Fr.
         Polyporus hirsutus Schw.
      c. Gilled mushrooms
         Collybia radicata Rehl.
         Armillaria mellea Vahl.
         Pleurotus ostreatus Jacq.
         Hypholoma sublateritium Schaeff.
         Hypholoma perplexum Pk.
         Clitopilus abortivus B & C.
         Mycena Leajana Berk.
         Coprinus atramentarius (Bull.) Fr.
         Collybia platyphylla Fr.
      d. Puff-balls
         Lycoperdon pyroforme Schaeff.
         Scleroderma aurantium (Vaill.) Pers.
      e. Gelatinous fungi
         Tremella mesenterica Retz.
         Exidia glandulosa (Bull.) Fr.
      f. Chestnut blight
         Endothia parasitica (Murr.) Ander. and Ander.
   B. Common fungi (not in order of abundance)
      a. Woody and leathery polypores
         Polyporus lucidus (Leys.) Fr.
         Polyporus sulphureus (Bull.) Fr.
         Fomes fomentarius Fr.
         Polyporus brumalis (Pers.) Fr.
      b. Gilled mushrooms
         Amanita verna Fr.
         Amanitopsis vaginata Roze.
         Claudopus nidulans (Pers.) Pk.
         Clitocybe illudens Schw.
         Clitocybe infundibuliformis Schaeff.
         Collybia velutipes Curt.
         Collybia strictipes Pk.
         Coprinus micaceous (Bull.) Fr.
         Crepidotus versutus Pk.
         Gomphidius rhodoxanthus Schw.
         Hypholoma appendiculatum Bull.
         Lepiota procera Scop.
         Marasmius rotula Fr.
         Marasmius siccus (Schw.) Fr.
         Mycena haemotopoda Pers.
         Mycena galericulata Scop.
         Omphalia campanella Batsch.
         Pholiota adiposa Fr.
         Pleurotus sapidus Kalchb.
         Pleurotus serotinoides Fr.

Pluteus cervinus Schaeff.
Russula emetica Fr.
Russula fragilis Fr.
Russula mariae Pk.
Strobilomyces strobilaceus Berk.

c. Boletaceae
Boletus felleus Bull.
Boletus edulis Bull.
Boletus peckii Frost.
Boletinus porosus (Berk.) Pk.
Fistulina hepatica Fr.

d. Puff-balls
Geaster triplex Jungh.
Lycoperdon gemmatum Batsch.

e. Coral fungi
Clavaria flava Schaeff.
Clavaria cinerea Bull.

f. Spore-sac fungi (Ascomycetes)
Peziza coccinea Jacq.

C. Uncommon to rare fungi (not in order of abundance)

a. Gilled mushrooms

Agaricus sylvaticus Schaeff.
Amanita flavorubescens Atk.
Amanita rubescens Fr.
Armillaria amianthina Fr.
Cantherellus cibarius Fr.
Cantherellus umbonatus Fr.
Clitocybe albissima Pk.
Clitocybe clavipes Pers.
Clitocybe fragrans Sow.
Clitocybe multiceps Pk.
Clitocybe nebularis Batsch.
Clitocybe odora Bull.
Clitocybe subcyathiforme Pk.
Clitopolis orchella Fr.
Collybia confluens Pers.
Collybia dryophila Fr.
Coprinus comatus Fr.
Cortinarius distans Pk.
Crepidotus applanatus Fr.
Crepidotus malachius B & C.
Entoloma jubatum Pk.
Entoloma rhodopolium Fr.
Flammula flavida Fr.
Flammula spumosa Fr.
Hygrophorus ceraceus Fr.
Hygrophorus fulgineus Frost.
Hygrophorus pratensis Fr.
Hygrophorus conicus Fr.
Hypholoma hydrophilum Fr.
Hypholoma rugocephalium Atk.
Lactarius chrysorheus Fr.
Lactarius fuliginosus Fr.
Lactarius hysginus Fr.
Lactarius subdulcis Fr.
Lactarius vietus Fr.
Lentinus ursinus Fr.
Lepiota acutaesquamosa Fr.
Lepiota cristata Fr.
Lepiota naucina Fr.
Leptonia formosa Fr.

Agaricus sylvicola Vitt.
Amanita muscaria L.
Amanita solitaria Bull.
Cantherellus aurantiacus Fr.
Cantherellus rosellus Pk.
Clitocybe adirondackensis Pk.
Clitocybe candida Bres.
Clitocybe cyathiforme Fr.
Clitocybe laccata Scop.
Clitocybe multiformis Pk.
Clitocybe ochropurpurea Berk.
Clitocybe pieceina Pk.
Clitopolis noveboracense Pk.
Collybia butyracea Fr.
Collybia colorea Pk.
Collybia tuberosa Fr.
Cortinarius alboviolaceus Fr.
Cortinarius duracinus Fr.
Crepidotus fulvotomentosus Pk.
Darcomyces deliquescens (Bull.) Duby.
Entoloma niderosum Fr.
Entoloma strictus Pk.
Flammula lenta Fr.
Hygrophorus cantherellus Schw.
Hygrophorus chlorophanus Fr.
Hygrophorus miniatus Fr.
Hygrophorus coccineus Schaeff.
Hypholoma echinoceps Atk.
Hypholoma lachrymabundum Fr.
Inocybe radiata Pk.
Lactarius cinereus Pk.
Lactarius helvus Fr.
Lactarius piperatus Scop.
Lactarius trivialis Fr.
Lactarius volemus Fr.
Lenzites betulina Fr.
Lepiota clypeolaria Fr.
Lepiota metulaespora B & Br.
Leptonia asprella Fr.
Marasmius delectans Morg.

Marasmius elongatipes Pk.
Marasmius spongiosus B & C.
Mycena albolutea Pk.
Mycena cohaerens Fr.
Mycena minutula Pk.
Mycena polygramma Bull.
Mycena pura Fr.
Nolanea pascua Fr.
Panus strigosus B & C.
Panus stypticus Fr.
Paxillus lepista Fr.
Pholiota erebia Fr.
Pholiota mutabilia Fr.
Pholiota spectabilis Fr.
Pholiota squarrosoides Pk.
Pleurotus petaloides Bull.
Pluteolus reticulatus Fr.
Pluteus granularis Pk.
Russula alutacea Fr.
Russula lepida Fr.
Russula pusilla Pk.
Russula sordida Pk.
Russula uncialis Pk.
Russula vinosa Lindb.
Tricholoma laterarium Pk.
Volvaria bombycina Schaeff.
Marasmius oreades Fr.
Marasmius velutipes B & C.
Mycena alkalina Fr.
Mycena filopes Fr.
Mycena peliantha Fr.
Mycena pulcherrima Pk.
Nectria cinnibarina (Tode.) Fr.
Omphalia fibula Fr.
Panus rudis Fr.
Panus torulosis Fr.
Paxillus panuoides Fr.
Pholiota marginata Batsch.
Pholiota praecox Pers.
Pholiota squarrosa Müll.
Pleurotus corticatus Fr.
Pleurotus ulmarius Fr.
Pluteus admirabilis Pk.
Pluteus longistriatus Pk.
Russula foetans Fr.
Russula lutea (Huds.) Fr.
Russula purpurina Quel. & Sch.
Russula rubescens Beards.
Russula sanguinea Fr.
Stropharia squamosa (Pers.) Fr.
Tricholoma personatum Fr.

b. Boleti

Boletus alutaceus Morg.
Boletus chrysenteron Fr.
Boletus scaber Fr.
Boletus castaneus Bull.
Boletus diochrous Ellis.
Boletus subtomentosus Fr.

c. Puff-balls

Calvatia cyathiformis Bosc.
Lycoperdon echinatum Pers.
Cyathus striatus Willd.
Geaster hygrometricius Pers.
Lycoperdon subincarnatum Pk.

d. Spore-sac fungi (Ascomycetes)

Bulgaria inquinans Fr.
Gyromitra esculenta Fr.
Morchella esculenta Pers.
Peziza badia Pers.
Peziza scutellata
Geoglossum
Helvella crispa Fr.
Peziza aurantia Pers.
Peziza odorata Pk.
Xylaria polymorpha Pers.

e. Polypores

Daedalia ambigua Berk.
Daedalia confragosa Boton.
Merulius lachrymans (Jacq.) Fr.
Polyporus frondosus Fr.
Polyporus picipes Fr.
Polyporus squamosus Fr.
Favolus canadensis Klotsch.
Polyporus cinnibarinus Jacq.
Polyporus galactinus Berk.
Polyporus radicatus Schw.
Polyporus umbellatus Fr.

f. Other species

Clavaria amethystina Bull.
Clavaria inequalis Fl. Dan.
Clavaria muscoides Fr.
Clavaria aurea Schaeff.
Clavaria mucida Pers.
Clavaria vermicularis Scop.
Hydnum caput-ursi Fr.
Hydnum erinaceus Bull.
Hydnum septentrionale Fr.
Hydnum coralloides Scop.
Hydnum repandum (L.) Fr.
Tremella albida Huds.
Tremellodon gelatinosum Pers.
Hyroneola auricula-judae (L.) Berk.
Tremella lutescens Pers.
Tremalitelia nucleata (Seb.) Rea.
Craterellus cantherellus Schw.
Stereum sericium Schw.
Phallus ravenelii B & C.
Mutinus elegans (Mont.) Ed. Fischer.

1,500 species of the larger fungi should eventually be listed in such a forest as this. Of the woody sporophores that are persistent as brackets throughout the year, those of *Polyporus applanatus* are by far the most abundant. Usually these are the first of the brackets to appear upon newly fallen tree trunks, and often appear upon living trees. Even in such a case, however, they are probably growing on dead wood (Von Schrenk and Spaulding 1909). This fungus has been noted upon the decaying logs of practically all of the species of trees within the area.

Of the leathery polypores, *Polyporus versicolor* is in evidence everywhere, and usually its banded ruffles are the first fungus growth to appear upon fallen logs or branches of whatever species. *Stereum spadiceum* and *Polystictus pergamenus* may frequently be found in close competition with *Polyporus versicolor*. The service of these fungi and a few other closely related species in the forest under study in helping return to the soil the mass of woody plant débris which otherwise would continually accumulate can scarcely be overestimated. Bray (1915) points out that if it were not for some such disintegrating force at work in the forest, the surface of the ground would soon become clogged to such an extent as to make further plant growth impossible. Considering the number of species of fungi recorded at North Chagrin, and the great abundance of their sporophores at certain seasons, it is apparent that the humus must be thoroughly permeated with fungus mycelium, and that the fallen leaves, branches, and tree trunks are all "hot beds" of fungus activity.

The presence and the fruiting bodies of slime moulds (Myxomycetes) have been frequently noted, but no attempt has as yet been made to study their distribution or significance.

DYNAMICS OF SUCCESSION

Throughout the area the presence of old stumps, logs, and standing dead trees indicates something of the character of the forest of the recent past. Despite the passage of more than 60 years it is possible to recognize three species of trees represented by the stumps said to have been cut in 1871. These are oak (probably red oak, as this is the present most abundant species of oak), tulip, and chestnut. The species maps of tulip and red oak (Fig. 10) show both the living trees and the old stumps. It is apparent that red oak was formerly a constituent of the interior forest in much greater numbers than now. The 50 oak stumps that were measured showed an average diameter, without bark of sapwood, of 38.2 inches (97.03 cm.) at approximately 3 feet (91.44 cm.) from the ground. The average diameter of the 50 largest living red oaks is 30.2 inches (76.7 cm.) Apparently the stumps represent a considerably more mature stand than do the present trees.

There are 32 stumps of tulip recognizable at the present time. Measurements of these show an average diameter of 32.8 inches (83.31 cm.) without bark, at approximately 3 feet from the ground. The largest 32 living tulips show an average diameter of 29.6 inches (75.18 cm.), a size not greatly below that of the old stumps. A study of the species map (Fig. 10) indicates that the position of tulip in the community has changed little, if any, in the past 60 years.

The chestnut stumps cut in other years are few in number and are all located in present chestnut territory, indicating no recent movement of chestnut.

On the forest floor it is possible to recognize logs of beech, sugar maple, sassafras, tulip, tupelo,[2] cucumber, and hemlock. Of these, sassafras, cucumber, and hemlock are the only species that, from the position of the logs in the area, indicate a change in distribution as compared with the present. Of the standing dead trees, only cucumber and hemlock exhibit change of distribution. Sassafras and cucumber are apparently in process of being eliminated from the interior forest, as both formerly occurred there but are now practically limited to the spurs or their immediate vicinity (Fig. 10). Hemlock appears to be rapidly decreasing in numbers. Figure 12 shows the location of 85 standing dead hemlocks measuring from 10 inches (25.4 cm.) to 28.6 inches (73.2 cm.) in diameter. The discovery of the larvae of the flat-headed hemlock borer (*Melanophila fulvoguttata* Harr.) beneath the bark of many trees leads to the supposition that the activities of this insect is the immediate cause of the death of these otherwise apparently sound hemlocks. A comparison of Figure 12 with Figure 9 will show that these trees are in the heart of the present hemlock areas.

The rate of reproduction may have a large bearing upon the matter of stability or change in status of the forest constituents. The seeding of both beech and sugar maple is periodically abundant, but beech seedlings do not survive as well as those of sugar maple in the early stages of their development. In one area of approximately 25 feet (7.62 m.) square, 12 beech trees of from 2 to 4 seasons growth were counted, while the number of sugar maples of the same age in the same area was estimated to be in the neighborhood of 3,000—a proportion of 1 beech to 250 sugar maples. Yet the high mortality of young sugar maple saplings later seems to more than make up for this great difference in the early years of development. At present the seeding of both of these trees seems to be adequate to the needs of replacement of the species to make good the annual losses from the ranks of the old trees, and beech has the additional advantage of sending up suckers from the roots.

[2] Wherever "tupelo" is used in this paper the author refers to the common black gum, *Nyssa sylvatica* Marsh., and not *Nyssa aquatica* Marsh. which is most commonly called "tupelo" throughout the Southeast.—Ed.

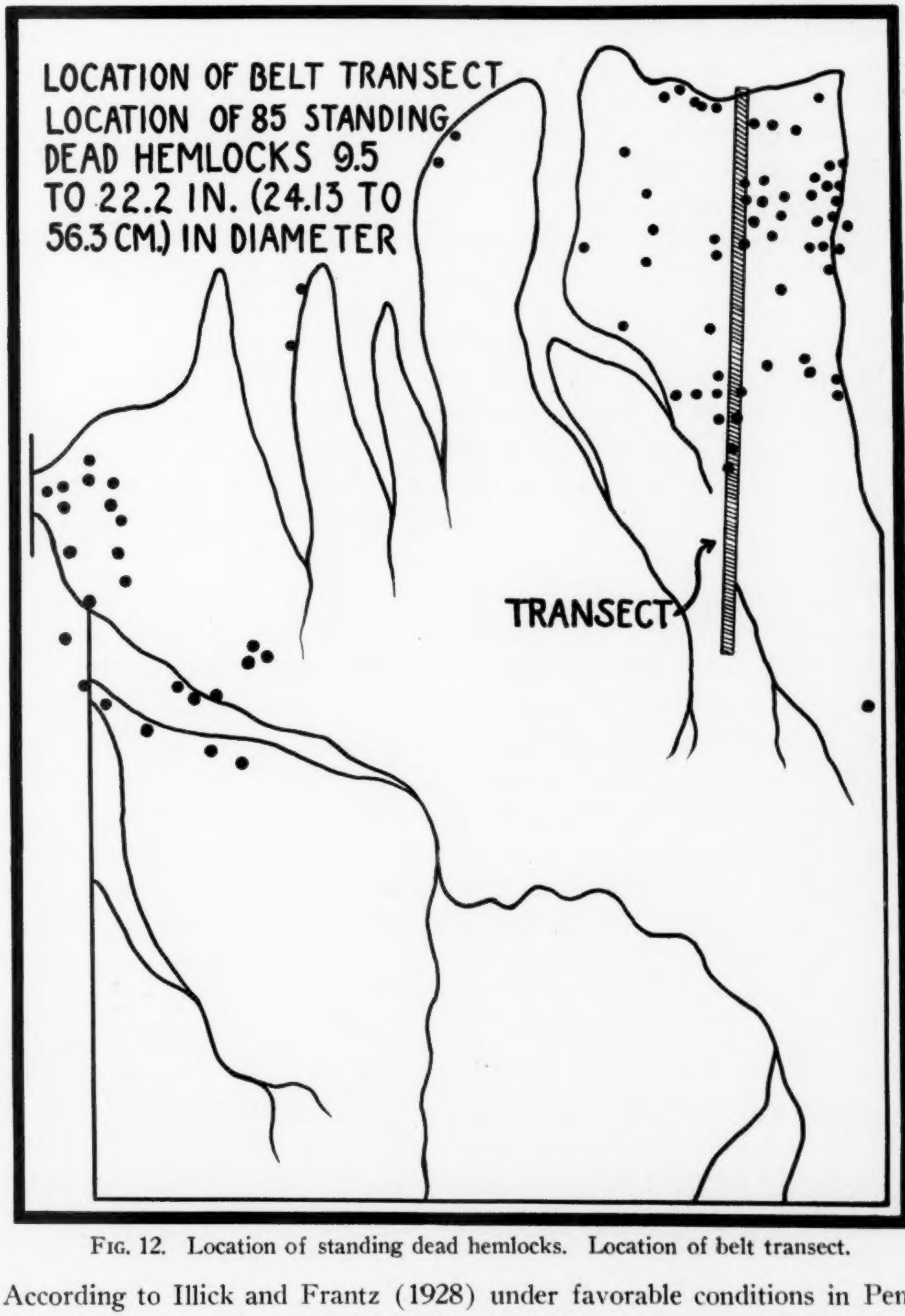

FIG. 12. Location of standing dead hemlocks. Location of belt transect.

According to Illick and Frantz (1928) under favorable conditions in Pennsylvania dense stands of beech will develop from root suckers alone.

While the seeding of red maple is at times very abundant, germination is poor, and seedlings and saplings do not survive in competition with those of beech and sugar maple.

The hemlocks of the area at times bear abundant crops of seeds, but germination has long been practically at a standstill. Apparently because of more favorable moisture conditions there was a fair amount of germination of hemlock seeds in 1935, but it remains to be seen whether or not a succeeding dry summer may wipe them out. In the hemlock areas it is quite noticeable that the dead leaves of beech and maple make up the bulk of the litter under the trees.

Both tulip and white ash bear seeds regularly and abundantly, and their seeds germinate well, but neither species long survives in competition with seedlings of beech and sugar maple. It is only in those places where sunlight has been let in, usually because of the fall of a large tree, that ash and tulip are able to raise their heads and make a place for themselves in the forest community. Under such conditions they make rapid growth.

Red oak and white oak often bear large quantities of acorns. Red oak in particular often so covers the ground with its seeds that they blanket everything else. Yet there are practically no oak seedlings or saplings of any kind in the forest.

The few hickories in the area produce good crops of nuts, yet there are no seedling or sapling hickories to be found away from the forest edge.

Cucumber and tupelo are regular seeders, and a considerable number of very young trees of these species are to be found in the neighborhood of the old trees. In addition, both of these species will sucker from exposed roots or the bases of stumps.

In order to study more definitely the relative significance of beech, sugar maple, and hemlock in the climax community, a belt transect was charted from a point in the beech-maple association on the higher ground, almost directly east to the edge of the bluff, thus traversing the entire width of the most extensive beech-hemlock territory in the area. Reference to Figure 12 will show its location.

The belt was 10 meters (32.8 feet) in width, and extended for a total distance of 360 meters (1181.1 feet). It was subdivided into 45 quadrats, each 10 by 8 meters (32.8 by 26.2 feet). The approximate position of all trees 2.5 cm (1 inch) or over in circumference was charted in each of these quadrats, and the trees measured breast high by tape. This chart is shown in Figure 13. A study of it reveals the following facts:

1. Beech is represented by large trees throughout the transect—32 of these ranging from 24 cm. (9.4 inches) to 80 cm. (31.5 inches) in diameter.

2. Sugar maple decreases in size as the hemlock area is approached, until it is represented only by saplings, and then soon drops out altogether.

3. Many decaying logs of hemlock on the ground are encountered before the present beech-hemlock association is reached. This condition persists well

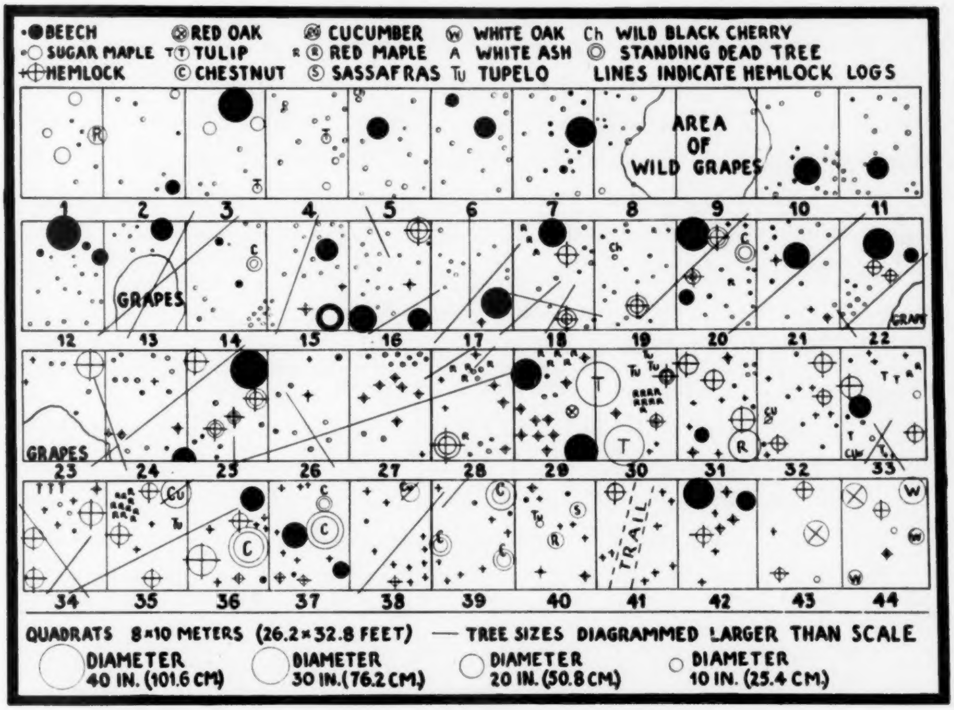

FIG. 13. Belt transect.

into the present beech-hemlock territory, but becomes less marked as the best hemlock development is reached. Practically all down timber in the transect is hemlock.

4. Reproduction of both beech and sugar maple, as represented by saplings and young growth in the transect is good. Reproduction of hemlock is poor—almost negligible.

5. The presence of large tulip, tupelo, cucumber, and chestnut is noted—the tulip outside the beech-hemlock territory, the other species associated with the hemlocks. The presence of oaks is noted as the edge of the bluff is reached.

6. Red maple appears as a rather constant but not important element in the transect.

A consideration of the age of the community under study may shed some additional light on the dynamics of succession. Table 8 shows the distribution of the most important tree species through certain size classes. It will be noted that all of the species here shown exhibit a peak of numbers in what might be called the middle size classes, with diminishing numbers toward both larger and smaller sizes. Although not shown in this table it is a fact that both beech and sugar maple show much larger numbers in smaller sizes than those included in Table 8. This is shown by the counts

recorded in Table 5, as well as by general observation. Sugar maple especially, in certain locations, has produced a tremendous number of saplings of from an inch to three inches in diameter. These dense stands of young maples are not of general distribution. They probably represent the heavy seeding of certain old trees under especially favorable circumstances in former years. Mortality among such young trees must be very great when a certain critical point in their development is reached, as Mr. Percy Parker, who has lived many years in the neighborhood, tells the writer that certain areas that are now practically clear of understory trees used to be densely crowded with sugar maple saplings when he used to hunt rabbits in these woods as a boy. In this connection it is interesting to note that one of the very areas thus pointed out by Mr. Parker and now devoid of young saplings, was recently covered (1935) with hundreds of thousands of sugar maple seedlings, standing so closely together as to provide a ground cover of continuous green throughout the summer, where in the previous years of this study the aspect had invariably been that of the almost unbroken brown of dead leaves.

It is of interest to note (Table 8) the decrease in numbers of individuals as the older trees (larger sizes) are considered. They seem to be approaching a limit of size that is rather definitely set.

TABLE 8. Numbers of trees in different size classes.

	DIAMETERS							
Inches	9.5 - 12	12 - 15	15 - 18	18 - 21	21 - 24	24 - 27	27 - 30	30 - 33
Centimeters	24.1 - 30.4	30.4 - 38.1	38.1 - 45.7	45.7 - 53.3	53.3 - 60.9	60.9 - 68.5	68.5 - 76.2	76.2 - 83.8
Beech	17	71	132	112	162	81	63	10
Sugar Maple	127	173	105	78	61	31	10	2
Red Maple	56	93	83	48	29	9	4	3
Hemlock	79	103	73	39	26	2	2	0
Chestnut	13	38	44	55	48	19	24	15
Tulip	29	19	4	1	6	5	4	5
White Ash	10	12	14	4	3	6	3	1
Red Oak	5	7	9	14	12	20	10	10

	DIAMETERS							
Inches	33-36	36 - 39	39 – 42	42- 45	45 - 48	48 - 51	......	63.2
Centimeters	83.8-91.4	91.4 - 99.0	99.0-106.6	106.6 - 114.3	114.3 - 121.9	121.9 - 129.5	......	160.5
Beech	9	4	3	1	..	..	..	..
Sugar Maple	1	1	0	1	..	..	..	..
Red Maple	3	2	1	1	..	..	..	..
Hemlock	0	0	0	0	..	..	..	..
Chestnut	6	3	2	2	..	..	..	..
Tulip	4	3	2	1	..	..	..	..
White Ash	2	0	0	0	..	..	..	..
Red Oak	3	0	2	0	1	1	..	1

To this the red oak seems to be the only exception, although it is probable that if it were not for the cutting of some large tulips in 1871 tulip would appear in sizes beyond those of the present table.

It has been possible to make counts of annual rings in a few cases of trees overturned in the area by a severe wind storm June 26, 1931. These records are shown in Table 9. In estimating the age of such a tree, a considerable period of time must be allowed for early stages of growth, as such trees growing from the forest floor, are greatly repressed during the early years.

TABLE 9. Counts of annual rings of trees overturned by storms.

Diameter at cut	Distance from cut to base of tree	Annual rings at cut	Estimated age of tree in years
BEECH			
22 in. (55.8 cm.)	43 in. (1.09 m.)	229	250
20 in. (50.8 cm.)	25 ft. (7.62 m.)	190	220
14 in. (35.5 cm.)	10 ft. (2.54 m.)	105	125
13.5 in. (34.3 cm.)	10 ft. (2.54 m.)	126	150
SUGAR MAPLE			
27 in. (68.6 cm.)	25 in. (76.2 cm.)	174	190
25 in. (63.5 cm.)	40 ft. (12.2 m.)	140	190
21 in. (53.3 cm.)	12 in. (30.5 cm.)	120	130
21 in. (53.3 cm.)	27 in. (68.6 cm.)	176	190
21 in. (53.3 cm.)	20 in. (50.8 cm.)	160	180
20.5 in. (52.1 cm.)	29 in. (73.7 cm.)	134	160
20 in. (30.8 cm.)	33 in. (83.8 cm.)	150	160
18 in. (44.7 cm.)	20 in. (50.8 cm.)	182	200
18 in. (44.7 cm.)	20 in. (50.8 cm.)	168	185
16 in. (40.6 cm.)	22 in. (55.8 cm.)	158	175
14 in. (35.5 cm.)	24 in. (61.0 cm.)	126	140
13 in. (33.1 cm.)	28 in. (71.1 cm.)	129	145
13 in. (33.1 cm.)	32 in. (81.3 cm.)	100	115
HEMLOCK			
22 in. (55.8 cm.)	20 in. (50.8 cm.)	164	175

A comparison of these tree sizes with the sizes of standing trees (Table 8) in the area shows that 39 per cent of the beeches and 13 per cent of the sugar maples making up this forest are as large, or larger, than the largest of which the annual rings were counted. This would indicate the age of the present forest to be well over 250 years.

The span of life of the sugar maple in this location seems to be determined by its size in relation to the soil. The humus is shallow, and the compact character of the subsoil seems to restrict the roots of this species to the soil above it—usually a matter of about 12 inches (30.5 cm.). Apparently few sugar maples above a certain size limit can long maintain them-

selves in this shallow soil against such severe wind storms as sometimes visit this forest. On the other hand, the life span of the beech seems to be determined by its susceptibility to fungus attack. There is probably no large beech tree in the area which is not hollow, at least at the base, the heartwood having been reduced to punk by the various species of fungi which seem to find an easy entrance to the tissues of this species. When finally the sapwood is affected, the tree will ultimately be twisted off its base by a wind storm, leaving the hollow stub standing. Apparently about 250 to 300 years is the limit of life for either the beech or the sugar maple in this location. There is need, therefore, for continual replacement of the dominants to make good the losses which more or less regularly occur.

The foregoing facts, taken together, clearly warrant the conclusion that in the area under study a gradual change in the status of the forest components has been in progress for some time, and the forces operating to bring about this change are operating at the present time. The conclusion that the hemlocks are being displaced by the beech and the sugar maple is inescapable. That the hemlocks formerly occupied much more territory than they now do is indicated by their remains in an area now completely occupied by the beech-maple association. In this movement the beech seems to play the leading part. Not only may beech hinder germination of hemlock by creating a humus unfavorable to the development of hemlock seedlings, but it may, by its dense shade, prevent the normal development of young hemlocks beneath its canopy, or by root competition in dry seasons reduce soil moisture available to neighboring hemlocks to the point where it ceases to be sufficient for hemlock requirements. The fact that beech roots more deeply than sugar maple in this environment may better fit it to play the part of entering wedge in displacing hemlock here. However, it may be expected that sugar maple will be more largely represented in this location in the future than it is now.

The need of plants for light is preëminent. Zon and Graves (1911) point out that early in life all plants are more or less tolerant of shade, but as they increase in size, their requirements for light become more and more definite, and that these requirements differ for different species. Burns (1923), studying the light requirements for 14 species of forest trees, found that each had a specific minimum requirement below which it could not live. The three trees with the lowest requirements he found to be, sugar maple lowest, beech next, and hemlock next. Daubenmire (1930), studying evaporation rate, light, soil acidity, and soil moisture under hemlock in Indiana, attempted to correlate the difference between hemlock and beech-maple. The results indicated an equal degree of mesophytism in the two associations. Studies of hemlock and its environment have been made by Moore, Richards, Gleason, and Stout (1924). While some slight differences were

found in the evaporation rate and in soil and air temperatures as compared with the hardwood forest, these do not seem significant enough to be recognized as controlling factors in the distribution of hemlock.

Apparently hemlock is not restricted in its location, as compared with the adjacent beech-maple association, by either temperature or moisture conditions, or by the chemical constitution of the soil; but rather, it is in process of elimination by competition within areas formerly occupied by it but now being gradually taken over by beech and sugar maple as dominants. The view that hemlock is thus being displaced is in accord with the opinion expressed by Weaver and Clements (1929) that the hemlocks of this region represent a remnant of the so-called "Lake Forest" to the north, returning with the retreat of the glacial ice, and now existing here only as small relict areas.

The fact that no chestnut saplings, and but very few smaller chestnut trees are to be found within the area, and that chestnut and hemlock were formerly very closely associated (Fig. 9) apparently on more or less even terms, leads the writer to the opinion that chestnut as well as hemlock would have fallen in competition with the beech-maple association, had not the "chestnut blight" wiped out the chestnuts before their time. For this reason chestnut may not be expected to "come back" in this environment naturally.

Undoubtedly the few oaks, hickories, sassafras, and other trees of subclimax types will gradually be eliminated through failure of reproduction, though sassafras has the great advantage of being able to reproduce by suckers from the roots. The presence of these trees, normally associated with the oak-chestnut forest, suggests an inter-relation of hemlock with oak-chestnut on the one hand, and beech-maple on the other, such as might have produced at one time an oak-chestnut-hemlock mictium which has now gone over to beech-hemlock.

That cucumber, and probably tupelo, have suffered displacement from the interior forest is clear, yet because of the steady though small reproduction rate of both species, and their commanding size when fully grown, they will probably continue for a long time as associates with the climax.

Secondary Succession

Under present conditions, the causes of secondary succession within the area are limited to denudations occurring by reason of the washing away of humus and top-soil at times of heavy rains, the slipping of earth and shale on the sides of the ravines due to erosion, and to the letting in of sunlight where breaks in the forest canopy occur because of the death of large trees which may either fall or remain standing, or whose tops or large branches may be broken off.

It is the uprooting of the large trees, exposing a more or less circular area of hard yellow clay, that causes most if not all of the secondary succession noted in the area by the writer. Such a depression may hold water for a large part of the year, and for this reason many seeds will not germinate upon it. From the edges of the torn mat of humus pokeweed is usually the first plant to appear. Commonly red-berried elder and high-bush blackberry are found along with the pokeweed. On the bare wet clay the spores of ferns, and the seeds of violets, wood sorrel, and great lobelia will germinate. Tulip and white ash frequently appear, but neither beech nor sugar maple will start on this surface.

From studies which have been started within the area in several localities where secondary succession is in process, but which cannot be reported on in detail here, it appears that tulip and white ash are the species that thrive, when the opportunty offers for rapid development in unoccupied territory. This accounts for the rather general distribution of these two species throughout the climax, both at the present time, and in the case of the tulip, formerly.

Ecological Classification of Plants

The dominant plants in any biotic community are considered to be those which, by reason of their size, abundance, and distribution, largely determine the conditions under which other organisms shall live in association with them. In the forest the dominants are usually trees. They are exposed directly to the sun, rain, snow, and wind; and other organisms mostly live underneath them. Beneath the trees temperature, light, evaporation rate, humidity, precipitation, wind, and other factors in the environment may be greatly modified. Only such plants and animals as are adapted to life under these conditions can exist here. The dominants therefore not only raise barriers against certain forms of plant and animal life—they invite others.

Primary dominants are those which, by reason of their wide and more or less even distribution and abundance, exercise their influence over the greater part of the community. Secondary dominants are those dominants which, by reason of their less frequent occurrence, do not exercise as great influence over the community as such. Their occurrence in the community, however, is rather regular. Incidental dominants, in this paper, are such trees as attain large size, and so exert an influence over a limited area, but which do not occur in numbers, or with any degree of regularity in the community. Subdominants are all other plants. They do not attain great size, but have adapted themselves to conditions of existence below the dominants. On this basis the plants of the area may be classified as in Table 10.

TABLE 10. Ecological classification of plants.

In beech-maple association	In beech-hemlock-oak-(chestnut) mictium	In ravines (flood-plain extensions)
	1. *Primary dominants*	
Beech Sugar Maple	Beech Hemlock (Chestnut)	Hemlock
	2. *Secondary dominants*	
Red Maple Tulip White Ash Northern Fox Grape	Red Maple Red Oak	
	3. *Incidental dominants*	
Shagbark Hickory Cucumber Red Oak White Oak	Shagbark Hickory Cucumber Tupelo Sassafras White Oak Wild Black Cherry Pignut Black Birch Scarlet Oak	American Elm Basswood Slippery Elm Butternut Black Walnut Bitternut
	4. *Sub- dominants*	
Hop Hornbeam American Hornbeam Shrubs, vines, herbs, ferns, and other plants, as listed in tables 6 and 7.	Hop Hornbeam American Hornbeam Flowering Dogwood Shadbush Shrubs, vines, herbs, ferns, and other plants as listed in tables 6 and 7.	Shrubs, vines, herbs, ferns, and other plants.

CHARACTER OF ANIMAL POPULATION

METHODS OF STUDY

Contrasted with the study of the plants of any area the study of its animal population presents an entirely different and much more difficult problem. Animals do not "stay put" as do plants. If the ecologist would really learn to know the animal content of an area, he must become so familiar with it that he feels thoroughly "at home" in it, and should achieve, in some degree at least, such a sympathetic attunement to the ebb and flow of its life activities that he becomes conscious of changes while they are in progress, and senses the significance of small matters as they arise. He must acquire the ability to move quietly and easily about, making a minimum of disturbance, while the senses of sight, hearing, and smell bring him information for his record.

While the methods of study of animals in their natural habitats must vary in accordance with the season, and often with the species studied, there are some general methods which, if carefully followed, should always offer a fair chance of definite returns. Such general methods as were used by the writer in this study were:

1. Regular and frequent visitation of the area. The writer was fortunately so situated that he could and did devote the Mondays of each week throughout the entire four years of this study to such visitation, with the exception of six scattered weeks, when observations were made by others under his direction. Familiarity with the area and its inhabitants was thus built up, and a picture of consecutive changes as they occurred secured, which probably could have been realized accurately in no other way. In addition to these extended weekly observations it was often possible to augment the record by more limited occasional visits in connection with other matters.

2. An increasing keenness of observation and interpretation of things seen and heard was deliberately sought after. A bird's feather on the ground, the scattered remnants of a meal, a dead shrew on a log, the droppings of animals, the barred owl's cast pellets, the character of woodpecker "workings," and many sounds and smells, all raised questions for which the correct answers were sought, even though considerable time might elapse between question and answer, and sometimes experiment was necessary for the solution of the problem.

Thus the presence of a heretofore unsuspected mammal (later confirmed by securing two specimens in the flesh) was determined through the discovery of the tiny jaw bone of the smoky shrew; and a method of ascertaining the presence of the seldom-seen flying squirrel was worked out by feeding hickory nuts to several species of captive squirrels, and noting that the flying squirrel, (and in fact the other species also) left a characteristic "signature" upon the nut shell.

3. Orderly routine in observation and recording on the spot. On each weekly visit the same course was followed, covering the entire area. Frequently the direction of travel was reversed, so that the same part of the area might be visited at different times. During this weekly survey an effort was made to identify accurately each species seen or heard; to make as complete a count of individuals as possible, or in the case of large numbers, to make a close estimate of numbers based on unit counts; to locate the occurrence of each individual on a small map carried for the purpose each week; to make notes of conditions of weather, changes in the plant or animal life observed, activities, relationships, or other facts considered significant. As this work was, with the few exceptions noted, always performed by the same person, usually alone, differences which might be due

to individual variances were eliminated, and the resultant data should be fairly comparable from one period to another. In estimating populations which are not restricted either to beech-hemlock or beech-maple environment, account does not have to be taken for what Leopold (1933) calls "blanks," as the entire area is essentially "forest" throughout. Even the area of the trails does not have to be figured out, as these are a very much used part of the habitat. All observations were recorded under appropriate headings on a temporary record carried for the purpose, and later transcribed to a permanent record, usually on the evening of the same day.

4. Concentration, at times, on special phases of animal behavior. Such were the studies of animal tracks in the snow, the location of the nesting territories of birds, and the home ranges of mammals, the study of food habits as special opportunities presented themselves, and the special study of the abundance and distribution of mice and shrews.

5. Visitation of the area at night. As the activities of some animals are carried on mainly after dark, it was considered of importance to visit the area a number of times, for varying periods, during the hours of darkness.

6. Observation of captive animals. While it is recognized that animals in captivity undoubtedly behave differently than in a state of natural freedom, it is also evident that much may be learned as to the character of the animal, and some understanding gained as to its equipment to meet competition in its natural environment, from a study of it at close quarters, even though under restraint. Opportunities were at hand during the summers to thus become acquainted with the New York weasel, raccoon, opossum, skunk, woodchuck, cottontail rabbit, red squirrel, chipmunk, flying squirrel, white footed mouse, pine mouse, barred owl, Cooper's hawk, red-tailed hawk, red-shouldered hawk, crow, and pilot blacksnake.

THE MAMMALS OF THE AREA

Table 11 gives the list of mammals whose presence in the area is known from direct observation. Representatives of all of these except the Virginia deer and the fox squirrel have been in the hands of the writer at various times, and skins of all of the species of mice, shrews, moles, bats, and chipmunk are deposited with the Cleveland Museum of Natural History. Scientific names are as given in the List of North American Recent Mammals, Bulletin 128 of the United States National Museum, with the exception of the eastern chipmunk, which is described by Howell (1929).

While the numbers and relative abundance of mammals in the area will always be subject to considerable fluctuation, the common species listed in Table 11 will usually be found in the order given; the most abundant being placed first. For the less common species enough information is not yet at hand to warrant an attempt to estimate abundance.

TABLE 11. The mammals of the area.

Common species	
Short-tailed Shrew	*Blarina brevicauda talpoides* (Gapper).
Northern White-footed Mouse	*Peromyscus leucopus noveboracensis* (Fischer).
Eastern Chipmunk	*Tamias striatus fisheri* Howell.
Northern Gray Squirrel	*Sciurus carolinensis leucotis* (Gapper).
Southern Red Squirrel	*Sciurus hudsonicus loquax* Bangs.
Small Eastern Flying Squirrel	*Glaucomys volans volans* (Linnaeus).
Cottontail Rabbit	*Sylvilagus floridanus mearnsi* (Allen).
Southern Woodchuck	*Marmota monax monax* (Linnaeus).
Eastern Raccoon	*Procyon lotor lotor* (Linnaeus).
Eastern Skunk	*Mephitis nigra* (Peale and Beauvois).
Virginia Opossum	*Didelphis virginiana virginiana* Kerr.
Eastern Red Fox	*Vulpes fulva* (Demarest).
Domestic Dog	
Domestic Cat	
Less common species	
Smoky Shrew	*Sorex fumeus fumeus* (Miller).
Hairy-tailed Mole	*Parascalops breweri* (Bachman).
Star-nosed Mole	*Condylura cristata* (Linnaeus).
Silver-haired Bat	*Lasionycteris noctivagans* (Le Conte).
Big Brown Bat	*Eptesicus fuscus fuscus* (Beauvois).
Red Bat	*Nycteris borealis borealis* (Müller).
New York Weasel	*Mustela noveboracensis noveboracensis* (Emmons).
Fox Squirrel	*Sciurus niger rufiventer* (Geoff.).
Pine Mouse	*Pitymys pinetorum scalopsoides* (Audubon and Bachman).
Meadow Mouse	*Microtus pennsylvanicus pennsylvanicus* (Ord).
Hudson Bay Jumping Mouse	*Zapus hudsonius hudsonius* (Zimmerman).
Woodland Jumping Mouse	*Napaeozapus insignis insignis* (Miller).
Virginia Deer	*Odocoileus virginianus virginianus* (Boddaert).

The above list of 25 mammals (omitting dog and cat) contains 49 per cent of the entire list of mammals (51) listed by the Ohio Department of Agriculture as now to be found in the State (Bull. 54, Bureau Scientific Research, 1931).

That the bison (*Bison bison* (Linnaeus)), American elk (*Cervus canadensis canadensis* (Erxleben)), Virginia deer (*Odocoileus virginianus virginianus* (Boddaert)), black bear (*Ursus americanus americanus* (Pallas)), and panther (*Felis cougar* Kerr) were once abundant in this region is attested by early writers. In view of the fact that all of these animals were completely exterminated from northern Ohio many years ago, it is interesting to find evidence of the return of one of them, the Virginia deer, to the locality. In view of the present overstocked condition of the deer ranges in western Pennsylvania (Clepper 1931) it would not be surprising to find deer wandering into northeastern Ohio from that direction.

DISTRIBUTION AND ABUNDANCE OF MAMMALS

In late July and early August 1932 some line trapping with spring mouse traps throughout the area demonstrated the very general distribution of short-tailed shrews and white-footed mice in all parts of the forest. It appeared that a catch could be made at every stump, or decaying log, or litter of sticks. Tunnels and runways were also found everywhere under the humus and

loose leaf-litter. Apparently the habitat was then occupied to the saturation point by mice and shrews. From a third to a half of the 98 animals trapped were either wholly or partially eaten, though the traps were inspected daily, and were usually under cover. This in itself indicated a large shrew population. The conditions of that autumn have not been duplicated since.

In late September and early October of the same year a more definite attempt was made to secure data that could be used as a basis for estimating the number of these two animals. Five quadrats were laid out in carefully selected territory, each 10 meters (32.75 feet) square. The location chosen for each was such as to make it typical of the whole area. Two were in beech-hemlock environment, and three were in beech-maple. One of the three in beech-maple environment had in it no stumps or logs or cover of any kind except the humus and leaf litter of the forest floor. The others included various types of shelter such as are commonly distributed over the area—tree roots, old logs, stumps and the like. Mouse traps of the usual spring-catch variety were used, baited with both oatmeal and raw beef, and usually set in groups of threes in runways that showed evidence of use, or in sheltered places. Trapping in each quadrat was continued until several days had passed without a catch. Usually this meant about two weeks of total time. It was then assumed that all of the mice and shrews using the quadrat as a hunting ground had been captured. Traps were inspected daily, often more frequently. Careful records were kept.

If the average catch of all five quadrats is taken as representing the population of an average 10 meter square for the whole area, then the population may be computed for any unit of the area. Later studies (unpublished) made by Mr. B. P. Bole, Jr., of the Cleveland Museum of Natural History, have demonstrated that the drift of small mammals from neighboring territory into the quadrat, especially at times when populations are high, is greater than was realized at the beginning of this study. It was originally felt that an offset existed in the loss of animals eaten and removed from the traps, large enough to counterbalance the entrance of others into the quadrat during trapping operations. The figures given in Table 13 for short-tailed shrews and white-footed mice are therefore undoubtedly too high, yet they are used in this paper as they establish a basis for comparisons with subsequent years during which the same trapping methods have been followed.

Accordingly, in September 1933 five quadrats of the same size as those used in 1932 were set up adjoining the quadrats of 1932, and trapped. The original five quadrats were again trapped in the autumn of 1934, and again in the autumn of 1935. Four consecutive groups of annual records were thus provided. In addition to indicating the distribution and abundance of short-tailed shrews and white-footed mice, these operations revealed the

presence of certain other species of small mammals—namely, Hudson Bay jumping mouse, woodland jumping mouse, pine mouse, meadow mouse, smoky shrew, and star-nosed mole. The results of the quadrat trapping are given in Table 12.

TABLE 12. Trapping records of mice and shrews.

Quadrats	A-beech-maple				B-beech-hemlock				C-beech-maple				D-beech-hemlock				E-beech-maple				Totals			
Years	'32	'33	'34	'35	'32	'33	'34	'35	'32	'33	'34	'35	'32	'33	'34	'35	'32	'33	'34	'35	'32	'33	'34	'35
Short-tailed shrew	10	4	2	8	12	0	0	2	5	3	1	4	6	2	1	5	4	3	2	4	37	12	6	23
White-footed mouse	8	1	0	3	3	0	0	5	6	0	0	4	5	3	1	7	6	1	3	8	28	5	4	27
Hudson Bay jumping mouse													1								1			
Woodland jumping mouse					1																1			
Pine mouse											2	5								2			2	7
Meadow mouse								1																1
Smoky shrew			1				1																2	
Totals	18	5	3	11	16	0	1	8	11	3	3	13	12	5	2	12	10	4	5	14	67	17	14	58

By reducing square meters to acres, and averaging the catch of all five quadrats annually for shrews and mice, an estimate of the numbers of these animals on an acreage basis may be secured. These figures are shown in Table 13. For convenience the estimated numbers of the other common mammals of the area are also shown in this table. These are based, not on trapping records, but on weekly counts of numbers, studies of tracks on the snow in winter, and other evidence. The fact that the two species of jumping mice do not appear from the trapping records to be of general distribution within the area, and the actual limits of their habitats being unknown at the present time, makes it impossible to include these species in the estimate. The occurrence of the meadow mouse in 1935 is considered not to represent a resident animal, but rather one migrating through the area. The four records of the occurrence of the smoky shrew (2 in traps, 1 jawbone found, remains of 1 in an insect trap) at widely separated points, two of which were in beech-hemlock, and two in beech-maple environment, suggest the general distribution of this animal throughout the area, and estimates of numbers are given. The case of the pine mouse presents an interesting situation. Previous to 1934 there was no evidence of the presence of this species in the area. The capture of 2 individuals (1 female, 1 immature male) in one quadrat well within the interior forest (beech-maple) in 1934 indicated small numbers and limited distribution. In 1935, although but 7 captures were recorded in the quadrats (Table 12), 12 others were caught in various ways (the writer caught one by hand) at such widely separated points within the area as to make it certain that the species was then well established in all parts of it.

TABLE 13. Common mammal population of the area—numbers of individuals.

Species	Autumn 1932			Autumn 1933			Autumn 1934			Autumn 1935		
	Per acre	*Per hectare	Total in area	Per acre	Per hectare	Total in area	Per acre	Per hectare	Total in area	Per acre	Per hectare	Total in area
Short-tailed shrew	299.45	739.6	19464.	97.12	239.8	6312.	48.56	119.9	3156.	187.	461.8	12165.
White-footed mouse	218.52	539.7	14203.	40.46	99.9	2629.	32.37	79.9	2104.	209.8	518.1	13635.
Pine mouse	......	......	......	......	......	......	8.1	19.8	525.	24.2	59.7	1575.
Chipmunk	10.0	24.7	650.	4.0	9.9	260.	10.0	24.7	650.	15.0	37.0	975.
Smoky shrew	......	......	......	......	......	......	8.1	19.8	525.	4.0	9.8	260.
Gray squirrel	0.03	0.07	2.	0.31	0.74	20.	0.9	2.2	60.	1.0	2.4	65.
Red squirrel	0.31	0.74	20.	0.23	0.57	15.	0.31	0.74	20.	0.5	1.2	30.
Cottontail rabbit	0.46	1.14	30.	0.61	1.48	40.	0.03	0.07	2.	0.06	0.15	4.
Flying squirrel	......	......	......	......	......	......	0.37	0.91	24.	0.37	0.91	24.
Woodchuck	0.15	0.37	10.	0.06	0.14	4.	0.09	0.22	6.	0.06	0.15	4.
Raccoon	0.18	0.45	12.	0.15	0.37	10.	0.18	0.45	12.	0.18	0.45	12.
Opossum	0.03	0.07	2.	0.06	0.14	4.	0.03	0.07	2.	0.03	0.07	2.
Skunk	0.09	0.22	6.	0.09	0.22	6.	0.00	0.00	0.	0.00	0.00	0.
Red fox	0.03	0.07	2.	0.06	0.14	4.	0.01	0.03	1.	0.03	0.07	2.
Totals per acre	529.25	......	......	143.15	......	......	109.05	......	......	442.23	......	......
Per hectare	......	1307.13	......	......	353.40	......	......	268.79	......	......	1091.80	......
Total in area	......	......	34401.	......	......	9304.	......	......	7087.	......	......	28753.

*1 hectare = 2.47 acres.

The status of the moles and the bats in the area is not clear. The subsoil is ill-suited to the work of moles because of its hardness, and though earthworms are noted in the humus and in the soft wood of decaying logs, the tunnels of moles are rarely evident. Perhaps the loose leaf-litter may effectually conceal them. On the other hand, when the humus was reduced to the semblance of tinder during the dry spring and summer of 1933 and mole tunnels were for the first time noted in the drying stream-beds, they were few in number. For the present the writer assumes that the numbers of moles of all species in the area are quite limited. But two specimens have been taken, representing two species.

The bats are as elusive as the moles. Bats have never been noted in numbers, and only on the wing. They give the impression of passing over or through the area rather than of hunting within or over it. They are usually seen flying high, though Mr. Earl Cady reports having seen two large bats (big brown bats?) at 12:30 A.M. September 7, 1933, apparently busily feeding in the moonlight over a large patch of jewel-weed in the woods. In the latter part of August 1933 an attempt was made to determine at least the species of bats flying in the forest. Mr. Arthur B. Fuller of the Cleveland Museum of Natural History, on three different nights, by wing-shooting over a grape tangle in the beech-maple association, collected a total of 5 bats, of which 3 were big brown bats. Apparently this species is the common bat of the area.

FOOD CHAINS AND ECOLOGICAL NICHES

In summing up the relative importance of the mammals of the area account must be taken not only of their numbers, but also of the duration of the periods of their activity, and of their food-habits. Those mammals classed as the less common species (Table 11) are clearly of much less importance ecologically than are the common ones. If they were entirely removed from the area the probability is that little if any change would be apparent. Attention may therefore be centred upon the common species. Table 14 classifies these on the basis of duration of activities.

TABLE 14. Common mammals classified according to duration of activities.

	Active throughout the year	Active by day	Active by night	Inactive during winter
Short-tailed shrew	*	*	*	.....
White-footed mouse	*	.....	*	.....
Chipmunk	.....	*	.....	*
Gray squirrel	*	*	.....	.....
Red squirrel	*	*	.....	.....
Flying squirrel	*	.....	*	.....
Cottontail rabbit	*	*	*	.....
Woodchuck	.....	*	.....	*
Raccoon	.....	.....	*	*
Skunk	.....	.....	*	*
Opossum	.....	.....	*	*
Fox	*	*	*	.....

Probably the most ceaselessly active of these animals is the short-tailed shrew, though Shull (1907), who studied the habits of this mammal, expresses the opinion that "times of daylight are not selected by the shrew for its greatest activity." Yet the writer's observations do indicate considerable daylight activity for this little mammal. In the area under study the barred owl is a consistent hunter of the shrew by daylight. One can often locate shrews at work by the rustling movement of dry leaves on the forest floor by day as well as by night. Not infrequently one gets a glimpse of a shrew by day as he flashes from one opening of his tunnel to another, or he may sometimes be surprised at work by quickly removing or turning over the decayed log or piece of bark that serves as a roof for his runway. Traps set in the morning and inspected before dark frequently contain shrews. Sometimes the bait will be so quickly taken by shrews, after setting the trap in daylight, that the operator hears the snap as he turns away. That shrews are active at all seasons of the year is indicated by their tunnels under the snow, and their trails on its surface in winter.

Although the shrew is usually referred to as an insectivore, ecologically he might just as well be classed as a carnivore, for he is a hunter after fresh meat in any form, and in proportion to his size he needs a great deal of it. Shull (1907), studying the short-tailed shrew in a swampy habitat near

Ann Arbor, Michigan, found that in winter snails formed a part of the food supply. Meadow voles *(Microtus)* were also an observed part of the diet. It was found that vegetable foods offered to captive shrews were invariably rejected.

On the basis of experiments with captive shrews, Shull estimated that one short-tailed shrew, in one month, will eat:

	Number	Per cent of total
Meadow mice or equivalent in mice	8	40
Adult insects (size of May beetles — Lachnosterna)	90	20
Insect larvae (size of May beetles — Lachnosterna)	78	20
Earthworms 4 cm. long, contracted	53	5
Snails	18	15

In a different habitat the relative availability of the different items in the diet would certainly influence the proportions consumed. At North Chagrin undoubtedly the proportion of mice eaten would run higher both in number and per cent of total, as *Peromyscus* is smaller than *Microtus*, and the supply of snails would be considerably less. It is also probable that the proportion of insects, millipeds, and the like would run higher. Smaller shrews, like *Sorex*, would also be preyed upon. It is important to recognize the short-tailed shrew as more than an eater of insects.

Occupying the position of the most abundant mammal in the area, being the only one that approaches constant activity by day and by night, and at all seasons of the year, requiring an enormous amount of animal food at all times, and having no real check upon numbers except the barred owl, the short-tailed shrew appears as probably the most influential mammal in the area. He acts as an efficient check upon the numbers of mice and other species of shrew, and takes out the humus and decaying logs and stumps an immense number of insects and their larvae and of other forms like millipeds, centipedes, sowbugs, and worms. It is not entirely fanciful to liken his network of under-cover tunnels and runways to a vast system of spiderwebs, laid down for the same purpose as the spider's web—the ensnaring of his prey.

From the standpoint of numbers and all-year-round activity the white-footed mouse probably ranks second in importance in the area. Compared with the shrew, the white-footed mouse does not exhibit the same kind of high-tension activity. Johnson (1926) found experimentally that forest deer mice *(Peromyscus)* were nocturnal, with a well marked rhythm of activity, sinking to a minimum during daylight hours and reaching a high degree normally during the hours of darkness. Unlike the shrew, the mouse is directly dependent upon plant products for his main support. Although a rodent, he is not a strict vegetarian, however, but consumes considerable animal material. All of the captive white-footed mice observed by the

writer have always eagerly accepted insect food. Snails also are probably eaten (Cahn and Kemp, 1929).

Checks upon undue increase in numbers of mice exist in the short-tailed shrew, as noted above; the barred owl, whose cast pellets found in the area frequently contain remains of *Peromyscus;* and in the larger mammals of the flesh-eating group—skunk, raccoon, opossum, weasel, and fox.

The chipmunk should undoubtedly be placed third in importance among the mammals of the area on the basis of number and general distribution, even though he withdraws from above-ground activities at certain seasons of the year. While popularly credited with being a complete hibernator (Anthony, 1928, p. 243), this is certainly not the case with the chipmunks in the area under study. Except for the winter 1932-33, when the chipmunk population at North Chagrin was reduced to a very low ebb, the writer has observed chipmunks abroad throughout the winter months, sometimes with the temperature as low as 10° F. (-12.2° C.), and has noted their tracks in the snow indicating great activity at certain times in winter. Counts of as many as 58 in one morning, and 63 in another, both in February, suggest anything but complete hibernation at that time. In fact the writer is of the opinion that the entire chipmunk population was aroused to a high pitch of excitement by mating activities at that particular time.

The periods of the chipmunk's greatest activity at North Chagrin are from the first week in May to the middle of July, and from the middle of September to late November if the weather is good. There is a period of retirement underground from mid-July through August which is probably correlated with the physiological condition of moulting and renewing of the pelage. Howell (1929) mentions the fact that out of 1,349 specimens of *Tamias* examined by him, very few moulting specimens have been found. This is no doubt due to the animal's disappearance during the period of moult, so that relatively few moulting specimens would be encountered by collectors. Schooley (1934) thinks this disappearance, reported by others but not observed by him, is due to the summer breeding season.

The chipmunk, like the mouse, is dependent mainly on vegetable matter for his food supplies but also takes animal matter (Howell 1929, Cahn and Kemp 1929, Seton 1909). Captive chipmunks observed by the writer ate with great avidity all insects offered, and shells of snails are commonly found among the refuse on their feeding tables. In May and June the chipmunks at North Chagrin do a great deal of "rooting" in the humus after such food as the tubers of spring beauty, dwarf ginseng, Indian cucumber, and squirrel corn, or the root-stocks of trillium. In the fall, beech nuts, sugar maple seeds, and other nuts and seeds are gathered and stored underground.

Checks on the numbers of chipmunks in the form of larger predators

are not very apparent. It is possible that the fox and the weasel may exercise some influence, but direct evidence is lacking. Chipmunk remains have not been found in the casts of the barred owl in the area, nor has the owl been observed to hunt chipmunks. Cats have been definitely observed stalking chipmunks. Possibly the pilot blacksnake may be a definite consumer of chipmunks in summer. Under favorable conditions of food supply there seems to be no reason why the chipmunk population should not occupy all available habitats in the area—and this indeed seems frequently to be realized. Competition would then act to prevent overpopulation.

The other squirrels—red squirrel, gray squirrel, and flying squirrel—are all consumers of nuts, seeds, and fruits, as well as of some animal matter. Captive flying squirrels and captive red squirrels, under the observation of the writer greedily ate all insects offered them. As a group the arboreal squirrels are important members of the community by reason of their almost continuous activity throughout the year and their steady consumption of basic forest food supplies. Their function as destroyers of large numbers of insects must not be overlooked. Competition between species and individuals apparently acts as an efficient check upon numbers.

The rabbit and the woodchuck are normally rather unimportant elements in the biota of the area because of their small numbers. If either should increase greatly in abundance, and maintain their increased numbers for any considerable period of time, they might have a significant relation to the vegetation of the area by reason of their food requirements. The rabbit especially, under such conditions, might affect greatly the character of forest seedling trees and saplings. Such a condition has apparently never occurred, however. The very apparent check upon both of these animals is the red fox, about whose dens the remains of woodchucks and rabbits are very commonly found. Hamilton (1935) mentions rabbits as constituting 22.1 per cent by bulk, of the food of 206 foxes in fall and winter in New York and New England, and woodchuck remains stand highest in the list for 31 fox dens examined by him in July and August.

With the exception of the short-tailed shrew, the carnivores of the area have a larger sphere of activity than the 65 acres under study. Yet their regular visitation of it, and their resident character to some extent in the case of certain individuals, means a very considerable influence in its biotic relationships. The raccoon, the skunk, and the opossum may be regarded as somewhat in the nature of additional checks upon the undue increase of the smaller mammals. They undoubtedly limit to some extent the numbers of birds nesting on or near the ground. They must also be recognized as large consumers of insects, and of the so-called "cold-blooded" animals—crayfish, frogs, salamanders, and snakes. Their periods of greatest activity

correspond with those of the "cold-blooded" animals, and raccoons are especially diligent hunters of this sort of fare.

The weasel and the fox provide still further checks upon the smaller mammal population, and the fox especially seems important in limiting the number of rabbits.

Taken as a group, the mammals of the area illustrate well the adaptations of animals to a forest environment. Omitting the dog and the cat, which are associated with the presence of man in the near vicinity, and the deer, which is an occasional visitor only, and the meadow mouse, which we may consider a transient visitor, it appears that the 23 species remaining consist of 5 squirrels, 4 mice, 1 rabbit, 1 woodchuck (all chiefly herbivores); 2 shrews, 2 moles, 3 bats (all chiefly insectivores); and the raccoon, opossum, skunk, weasel, and fox (all chiefly carnivores). The composition of the whole group then, may be roughly indicated as:

Herbivores, 48 per cent.
Insectivores, 30 per cent.
Carnivores, 22 per cent.

This arrangement, however, is only a species grouping and does not indicate food relationships with any degree of exactness. Probably the weasel is the most nearly strictly carnivorous animal on the list, and the rabbit and the woodchuck the most nearly strictly herbivorous ones. Undoubtedly the squirrels and the mice consume great quantities of insects along with their mainly herbivorous diet, and this is true also of most of the carnivores. Even the red fox is accredited as an insect eater (Dearborn, 1932, and Hamilton, 1935). The bats, no doubt, are strictly insectivorous, but the moles and shrews are carnivorous as well as insectivorous. Most of those classed as carnivores might also be classed as omnivores. But the gist of the matter is that plant products, insects, and other invertebrates, are the mainstay of the mammal population of the area, while to a more limited extent the smaller mammals themselves serve to support the larger ones.

In their occupation of the territory it is interesting to see how these mammals have occupied fully all available habitats. The moles occupy the deeper parts of the substratum, so far as it is available to them; the shrews have appropriated the loose humus and leaf litter of the forest floor, using the runways of mice and moles as well; the chipmunks are animals of the floor itself and the débris that lies upon it in the shape of old logs, stumps, and litter, though making their homes and storehouses in tunnels that reach into the subsoil itself; the mice are inhabitants of logs and stumps and hollow trees and other forest litter, and the white-footed mouse is a climber of trees as well; the red squirrel, with his headquarters usually under some stump or bunch of roots, also ascends the trees, and frequently builds a nest in a grapevine suspended aloft; the gray squirrel is the true arboreal animal

of the area, spending much time aloft, using aerial runways by preference, and having his winter quarters usually high above the ground in some hollow tree top; the flying squirrel is also an arboreal animal, extending his aerial highways beyond the limits of those of the gray squirrel by reason of his abilities as an aerial glider; and the bats complete the occupation of all available habitats by hunting through the air itself.

The larger mammals of the list are mainly hunters upon the surface of the ground, though the raccoon and the opossum are climbers, and the raccoon's winter quarters are usually high above ground.

This division of territory and diversity of diet makes possible the support of a large population of mammals adapted to the limitations of the habitat, provided basic food supplies are present in normal quantities. In this particular forest this means beech nuts, sugar maple seeds, herbaceous vegetation, insects and other invertebrates.

Such was the condition in the autumn of 1931. At that time apparently every available habitat within the area was occupied to its upper limit of capacity by the shrews, mice, chipmunks, and gray squirrels. There had been very large yields of beech nuts and sugar maple seeds the previous autumn, as well as this autmun. Food supplies were more than adequate for even the large population then occupying the territory.

Fluctuations in Numbers of Mammals

As Elton (1927) has pointed out, the chief cause of fluctuation in animal numbers is the unstability of the environment. This is well illustrated in the case of the area under study by what happened in the autumn of 1932. This was the time of almost complete failure of the beeches and sugar maples to produce seed. Whether the resting rhythm of these two trees normally coincides, or whether it does so only occasionally because of a difference in length of rhythm, remains for further studies to determine. At any rate, basic food supplies practically disappeared just before the winter of 1932-33.

There was little storage of food by chipmunks that autumn, and they went underground almost a month earlier than the previous year when storage activities ran well into the last of November. Although there was no observation of the activities of the white-footed mice, the absence of their accustomed food supplies would have produced more or less of the same condition with them, so far as storage of winter food was concerned. The red squirrels, as appeared later, gathered and stored large quantities of tulip seed cones, and some of them subsisted upon scarcely anything else during the entire winter, as indicated by the refuse about their middens as the winter progressed. Hemlock seeds were also used by the red squirrels, but there was a deficiency in yield of these seeds also. Mushrooms were

much used. Seeds of cucumber trees, usually shunned as articles of diet, were freely gathered, stored and eaten by red squirrels that winter. These animals are probably naturally resourceful in the discovery and use of foods outside the usual list, as the droppings of horses were twice noted in red squirrel middens. These must have been discovered and brought in from near-by bridle paths. The fact that the red squirrels did not occupy the territory as fully as did the other rodents was also in their favor, for it is a recognized fact that competition within the ranks of a species is always keener than between different species, as the needs of the individuals are then identical. But the red squirrels were able to and did expand their individual territories, spreading into parts of the area not previously occupied by them.

The gray squirrels left the area early. About 50 of these animals occupied the area the previous winter, producing enough young in spring to keep their numbers fairly constant. But in September they moved out, leaving one lone squirrel to face the famine alone. This individual was frequently noted during the winter following. He seemed to be subsisting on a few hickory nuts, red oak acorns, tulip seeds, and mushrooms. The writer even saw him sampling the hard woody bracket of *Polyporus applanatus*, and later noted that the marks of squirrels' teeth on these unpalatable fungi were not at all uncommon that winter.

An interesting fact in connection with this winter was the increase in numbers of cottontail rabbits within the area. Previously they had been noted about the edges of the forest. Now they extended their feeding grounds into all parts of the area. Numbers were probably doubled, increasing from 20 to 40, and there was much evidence of their activities in the "barking" of young trees, and nipping off of the terminal buds and twigs of thousands of small trees of beech, sugar maple, and red maple. This meant the destruction of many seedlings, but of course in most cases they would necessarily have been eliminated by competition later. The rabbits naturally were not affected by the failure of beech nuts and sugar maple seeds, as their food consists of bark, buds, twigs, and the green leaves of the ferns, *Carex,* and other woodland plants such as *Hepatica* and *Dentaria diphylla* whose leaves remain green all winter.

During this winter not a single chipmunk was seen above ground, where counts of as high as 58 in a morning had been made the previous winter and have been made since. The following spring it was apparent that very few chipmunks had survived the winter, as only a few individuals were noted where usually the woods should have been "alive" with them.

The situation with regard to mice and shrews was not fully realized until the following autumn (1933) when the second attempt to estimate numbers by trapping was made. Then it appeared that the mice had suffered

a decrease of over 80 per cent, and the shrews a decrease of over 65 per cent (Table 15). The reduction in numbers of mice must have reacted directly upon the numbers of shrews, as mice enter so largely into shrew diet.

The summer of 1933 proved to be an especially dry one. The months of June, July, and August were devoid of any effective rainfall (Fig. 5). Such precipitation as did occur came in the shape of more or less violent rainstorms, with rapid run-off of water, and quick drying out of the surface leaves on the forest floor, which afforded no relief to the very dry condition of the humus. The Amphibia, Mollusca, and soft-bodied insects and larvae either perished or went into aestivation. This again meant a shortening of food supplies for the shrews. The mice apparently suffered more than the shrews as indicated by the shift in relative numbers of the two species (Table 15). Not only was their accustomed winter food supply lacking, but the shrews, on shortened rations, due to the disappearance of the insects and other invertebrateas, must have turned to the mice as acceptable food with more persistence than usual.

TABLE 15. Decrease in numbers of mice and shrews.

	1932	1933	1934	1935
Total numbers (5 quadrats):				
Short-tailed shrew	37	12	6	23
White-footed mouse	28	5	4	27
Relative proportions (percentage of shrews to mice):				
Short-tailed shrew	58	70.6	60	46
White-footed mouse	42	29.4	40	54
Per cent of decrease as compared with 1932:				
Short-tailed shrew	....	67.6	83.8	37.5
White-footed mouse	....	81.4	85.2	4.0

With the short-tailed shrew present in the numbers indicated in the autumn of 1932 (Table 13), one has only to attempt to visualize the enormous amount of animal food necessary for its support to sense the shrew population collapsing under its own weight. This explains the avidity with which baits were taken that autumn; the speedy devouring of so many of the animals trapped; the extension of runways into almost every square foot of ground; the absence in the traps of any other species of shrew. So far as the writer's observation goes, the only real check upon the numbers of shrews in the area was one pair of barred owls and their two young. All barred owl pellets thus far found in the area have, without exception, contained skulls or jaws of *Blarina brevicauda* as well as other material.

If, under optimum conditions, such as apparently existed in 1932, the shrew population got "out of bounds," so to speak, in the absence of sufficiently strong checks, then competition within the species itself would auto-

matically operate to reduce numbers. But as has been indicated, other and even more potent forces were already at work.

Coincident with the increase in the number of rabbits in 1932, there was an increase in the number of foxes hunting in the area, as shown by tracks in the snow in the winter of 1932-33. The number of rabbits was estimated at 40 in January, 1933. On January 15, 1934, with a fine tracking snow on the ground for several days, it was apparent that only 2 rabbits were then inhabiting the area. On the other hand the snow showed the presence of at least 4 hunting foxes—two more than the previous winter. Perhaps the decimation of the numbers of mice and squirrels which may be looked upon as "buffer food," had compelled closer attention to rabbit hunting on the part of the fox population. It is a recognized fact that there always seems to be a perceptible lag in the abundance of the carnivore as related to abundance of food supply (Elton 1927). The record of the snow the following winter (1934-35) showed one fox and no rabbits in the area.

The total disappearance of the skunk following the great reductions in numbers of mice, and the drying out of the humus insects in the summer of 1933 is another significant correlation. So also is the reduction in numbers of the pilot blacksnake.

The yield of beech nuts was again ample in the autumn of 1933 and of 1934, but the sugar maple did not come into bearing again until 1934. The first mammal to show recovery in numbers from the disturbed conditions of 1932 was the chipmunk. There was apparently a small spring brood, and also a summer brood, in 1933; the usual winter activity and a large emerging chipmunk population in the spring of 1934. Apparently numbers were completely recuperated during 1934, and the area seemed to have about all the chipmunks it would normally support. But 1935 proved this assumption wrong, for numbers were again increased. Incidentally this was true not only of the area under study, but chipmunks reached abnormally large numbers throughout the Chagrin valley and elsewhere in the vicinity of Cleveland. The speedy return of the species to normal numbers in the area under study is a notable demonstration of rapid response to favorable conditions in the environment. These must have been close to optimum to have produced such a result.

On the other hand the numbers of shrews and mice continued to drop, so that in the autumn of 1934 trapping records showed a decrease of over 16 per cent for the shrews and almost 4 per cent for the mice as compared with 1933. The shrews were now apparently suffering more than the mice, which would be expected because of the complete restoration of food supplies for the mice but not for the shrews.

The appearance of the pine mouse and the smoky shrew in the traps for the first time (1934), when the numbers of their arch competitor and prob-

able deadly enemy the short-tailed shrew was reduced to a comparatively low figure, seems to indicate that these animals may prosper only when the numbers of the short-tailed shrew are relatively small. Possibly their curve of abundance may fluctuate inversely with that of the short-tailed shrew.

The year 1935 proved to be a "mouse year" at North Chagrin. It witnessed the return of the white-footed mouse to numbers within 4 per cent of the high figures of 1932. The short-tailed shrew showed a substantial increase in numbers over 1934, but was still 37.5 per cent below 1932 numbers. This shift in relative proportions (Table 15) made the white-footed mouse, for the first time during the four years of this study, the most abundant mammal of the area. A new mammal, the pine mouse, appearing first in 1934, became common in the area. As evidence of the pressure of numbers of mice outside the area, the meadow mouse, not normally found in the forest, appears far within the forest boundaries.

Although the foregoing discussion of fluctuations in numbers of mammals is far from complete, yet enough evidence seems to have come to the surface to show how far-reaching a disturbance of the so-called "balance" of nature may be. In this case the disturbance is partly the normal rest in the bearing rhythm of the forest dominants, and partly the abnormal break in the climatic factor of precipitation of moisture. Only in the case of the skunk is there any direct evidence of disease having been a factor in the situation. Competition between individuals and between species seems to have been largely the keen-edged instrument whereby numbers were cut down after the failure of basic food supplies.

The Birds of the Area

As contrasted with the mammals, the birds of the area constitute at times a very rapidly shifting element in the community. From the standpoint of time spent within the area the birds may be divided into the following groups. Scientific names and the order of listing are as given in the American Ornithologists' Union Check List of North American Birds, Fourth Edition, 1931.

TABLE 16. Birds of the area by seasonal groups.

1. Permanent residents

(Species found in the area throughout the year)

Eastern Ruffed Grouse	*Bonasa umbellus umbellus* (Linnaeus).
Northern Barred Owl	*Strix varia varia* Barton.
Northern Pileated Woodpecker	*Ceophloeus pileatus abieticola* Bangs.
Red-bellied Woodpecker	*Centurus carolinus* (Linnaeus).
Eastern Hairy Woodpecker	*Dryobates villosus villosus* (Linnaeus).
Northern Downy Woodpecker	*Dryobates pubescens medianus* (Swainson).
Blacked-capped Chickadee	*Penthestes atricapillus atricapillus* (Linnaeus).
Tufted Titmouse	*Baeolophus bicolor* (Linnaeus).
White-breasted Nuthatch	*Sitta carolinensis carolinensis* Latham.
Eastern Cardinal	*Richmondena cardinalis cardinalis* (Linnaeus).
Red-eyed Towbee	*Pipilo erythrophthalamus erythrophthalamus* (Linnaeus).

2. Autumn and winter visitors

(Species found more or less continuously in the area only in the autumn and winter months)

Northern Blue Jay	*Cyanocitta cristata cristata* (Linnaeus).
Red-breasted Nuthatch	*Sitta canadensis* Linnaeus.
Brown Creeper	*Certhia familiaris americana* Bonaparte.
Winter Wren	*Nannus hiemalis hiemalis* (Vieillot).
Carolina Wren	*Thryothorus ludovicianus ludovicianus* (Latham).
Eastern Golden-crowned Kinglet	*Regulus satrapa satrapa* Lichtenstein.
Eastern Goldfinch	*Spinus tristis tristis* (Linnaeus).
Slate-colored Junco	*Junco hyemalis hyemalis* (Linnaeus).

3. Summer residents

(Species found continuously in the area only during spring and summer)

Northern Crested Flycatcher	*Myiarchus crinitus boreus* Bangs.
Eastern Phoebe	*Sayornis phoebe* (Latham).
Acadian Flycatcher	*Empidonax virescens* (Vieillot).
Eastern Wood Pewee	*Myiochanes virens* (Linnaeus).
Eastern Robin	*Turdus migratorius migratorius* Linnaeus.
Wood Thrush	*Hylocichla mustelina* (Gmelin).
Yellow-throated Vireo	*Vireo flavifrons* Vieillot.
Red-eyed Vireo	*Vireo olivacea* (Linnaeus).
Black-throated Green Warbler	*Dendroica virens* (Gmelin).
Cerulean Warbler	*Dendroica cerulea* (Wilson).
Oven-bird	*Seiurus aurocapillus* (Linnaeus).
Louisiana Water Thrush	*Seiurus motacilla* (Vieillot).
Hooded Warbler	*Wilsonia citrina* (Boddaert).
American Redstart	*Setophaga ruticilla* (Linnaeus).
Scarlet Tanager	*Piranga erythromelas* Vieillot.
Rose-breasted Grosbeak	*Hedymeles ludovicianus* (Linnaeus).

4. Transients

(Species found in the area only during their spring or autumn migration)

Yellow-bellied Sapsucker	*Saphyrapicus varius varius* (Linnaeus).
Yellow-bellied Flycatcher	*Empidonax flaviventris* (Baird and Baird).
Eastern Hermit Thrush	*Hylocichla guttata faxoni* Banga and Penard.
Olive-backed Thrush	*Hylocichla ustulata swainsoni* (Tschudi).
Gray-cheeked Thrush	*Hylocichla aliciae aliciae* (Baird).
Wilson's Thrush	*Hylocichla fuscescens fuscescens* (Stephens).
Eastern Ruby-crowned Kinglet	*Corythylio calendula calendula* Baird.
Blue-headed Vireo	*Vireo solitarius solitarius* (Wilson).
Black and White Warbler	*Mniotilta varia* (Linnaeus).
Blue-winged Warbler	*Vermivora pinus* (Linnaeus).
Nashville Warbler	*Vermivora ruficapilla ruficapilla* (Wilson).
Magnolia Warbler	*Dendroica magnolia* (Wilson).
Black-throated Blue Warbler	*Dendroica caerulescens caerulescens* (Gmelin).
Myrtle Warbler	*Dendroica coronata* (Linnaeus).
Blackburnian Warbler	*Dendroica fusca* (Müller).
Chestnut-sided Warbler	*Dendroica pennsylvanica* (Linnaeus).
Bay-breasted Warbler	*Dendroica castanea* (Wilson).
Blackpoll Warbler	*Dendroica striata* (Forster).
Connecticut Warbler	*Oporornis agilis* (Wilson).
Canada Warbler	*Wilsonia canadensis* (Linnaeus).
Eastern Purple Finch	*Carpodacus purpureus purpureus* (Gmelin).
White-throated Sparrow	*Zonotrichia albicollis* (Gmelin).
Eastern Fox Sparrow	*Passerella iliaca iliaca* (Merrem).

5. Occasional visitors

(Species noted only occasionally in the area)

Turkey Vulture	*Cathartes aura septentrionalis* Wied.
Sharp-shinned Hawk	*Accipiter velox velox* (Wilson).
Cooper's Hawk	*Accipiter cooperi* (Bonaparte).

Eastern Red-tailed Hawk	*Buteo borealis borealis* (Gmelin).
Broad-winged Hawk	*Buteo platypterus platypterus* (Vieillot).
Eastern Bob-white	*Colinus virginianus virginianus* (Linnaeus).
American Woodcock	*Philohela minor* (Gmelin).
Eastern Mourning Dove	*Zenaidura macroura carolinensis* (Linnaeus).
Yellow-billed Cuckoo	*Coccyzus americanus americanus* (Linnaeus).
Great Horned Owl	*Bubo virginianus virginianus* (Gmelin).
Eastern Whip-poor-will	*Antrostomus vociferus vociferus* (Wilson).
Eastern Nighthawk	*Chordeiles minor minor* (Forster).
Chimney Swift	*Chaetura pelagica* (Linnaeus).
Ruby-throated Hummingbird	*Archilochus colubris* (Linnaeus).
Northern Flicker	*Colaptes auratus luteus* Bangs.
Purple Martin	*Progne subis subis* (Linnaeus).
Eastern Crow	*Corvus brachyrhynchos brachyrhynchos* Brehm.
Starling	*Sturnus vulgaris vulgaris* (Linnaeus).
Bronzed Grackle	*Quiscalus quiscala aeneus* Ridgway.
Eastern Cowbird	*Molothrus ater ater* (Boddaert).
Canadian Pine Grosbeak	*Pinicola enucleator leucura* (Müller).
Eastern Blue Grosbeak	*Guiraca caerulea caerulea* (Linnaeus).
Indigo Bunting	*Passerina cyanea* (Linnaeus).
Common Redpoll	*Acanthis linaria linaria* (Linnaeus).
Red Crossbill	*Loxia curvirostra pusilla* Gloger.

The fact that the blue jay and the Carolina wren are included in the above list as autumn and winter visitors, rather than as permanent residents, may seem strange to one familiar with the birds of the Cleveland region, yet from the standpoint of the forest areas under study this is their status. The record of the blue grosbeak is unusual— a single record of a pair observed by the writer under favorable conditions May 15, 1933, in one of the grape tangles of the area.

Distribution and Abundance of Birds

Those birds nesting in the beech-hemlock environment only were the black-throated green warbler and probably the ruffed grouse. Those nesting in both beech-maple and beech-hemlock were the wood pewee, wood thrush, and ovenbird. The other species on the lists of permanent and summer residents nested exclusively in the beech-maple association. Most of the transient species were observed in beech-maple environment, while the winter bird companies roamed about the whole area.

The transient species, with the exception of the robins, thrushes, and certain warblers, do not bulk large in numbers. Estimates of 500 robins, 200 thrushes, and 300 warblers have been made at certain times. Autumn and winter visitors are irregularly present except in the case of the slate-colored junco and red-breasted nuthatch. Flocks of from 50 to 60 juncos have been noted, and the red-breasted nuthatch, present in alternate years, sometimes totals 50 to 60 in number.

The permanent resident species became quite well known. The number of hairy and downy woodpeckers, chickadees, tufted titmice, and white-breasted nuthatches are augmented considerably at times during the winter. Whether or not the actual birds nesting in the area in summer are present also in winter is not definitely known. Butts (1930) determined by band-

ing methods that individual chickadees, banded in winter, nested in or quite near their winter feeding territory, and that individual white-breasted nuthatches nested within or very close to their winter feeding area.

The barred owl, the pileated woodpecker, the ruffed grouse, and the cardinal are not usually present in greater numbers in winter than in summer. The towhees congregate in the woods in winter, but in spring most of them leave the area. These probably constitute the towhees nesting just outside the forest, though usually a pair or so may be found nesting just inside the forest edge.

Careful records of the numbers of birds observed on the weekly surveys of the area have been kept over the entire period of this study. The observed occurrence of the bird has been located on a map of the area carried each week for the purpose. Thus the species-constitution, numbers, and territories of the winter bird companies have been determined, the distribution of species and individuals noted, and summer nesting territories charted. While these figures (on their face) reflect seasonal fluctuations, they need considerable interpretation when it comes to studying absolute abundance. Weather conditions influence the count greatly at times. High winds, and storms of snow or rain reduce the number of birds observed. The appearance of the foliage on the forest trees in May is comparable to the dropping of a heavy curtain so far as visibility is concerned. Then sight records are largely replaced by those of hearing. When the song period is over it is quite difficult at times to get evidence of the presence or absence of birds. Chickadees, titmice, nuthatches, and woodpeckers become furtive and inconspicuous at the approach of, and during the nesting season. Differences in weekly counts at times reflect changes in activities or behaviour rather than fluctuations in abundance.

Perhaps the most reliable index to abundance of birds is the record of nesting pairs. By the use of the weekly maps, described above, it is possible to build up a series of maps (one for each species) covering the nesting season, which will show concentrations of records about certain localities. The localities thus indicated may be considered as within the territories of breeding pairs, and it is thus possible to estimate the numbers of breeding pairs of birds throughout the entire area and the approximate extent of the territory occupied by each. Figure 14 is presented as an illustration of this method, the species chosen being the hooded warbler, one of the common nesting species of the area. As nests are actually found, even though it may be during the following winter, their location with reference to the recorded location of the individual birds on the map makes it appear that this method may be relied upon to reveal the presence of a nesting pair or lone male, and fix the approximate limits of the nesting territory.

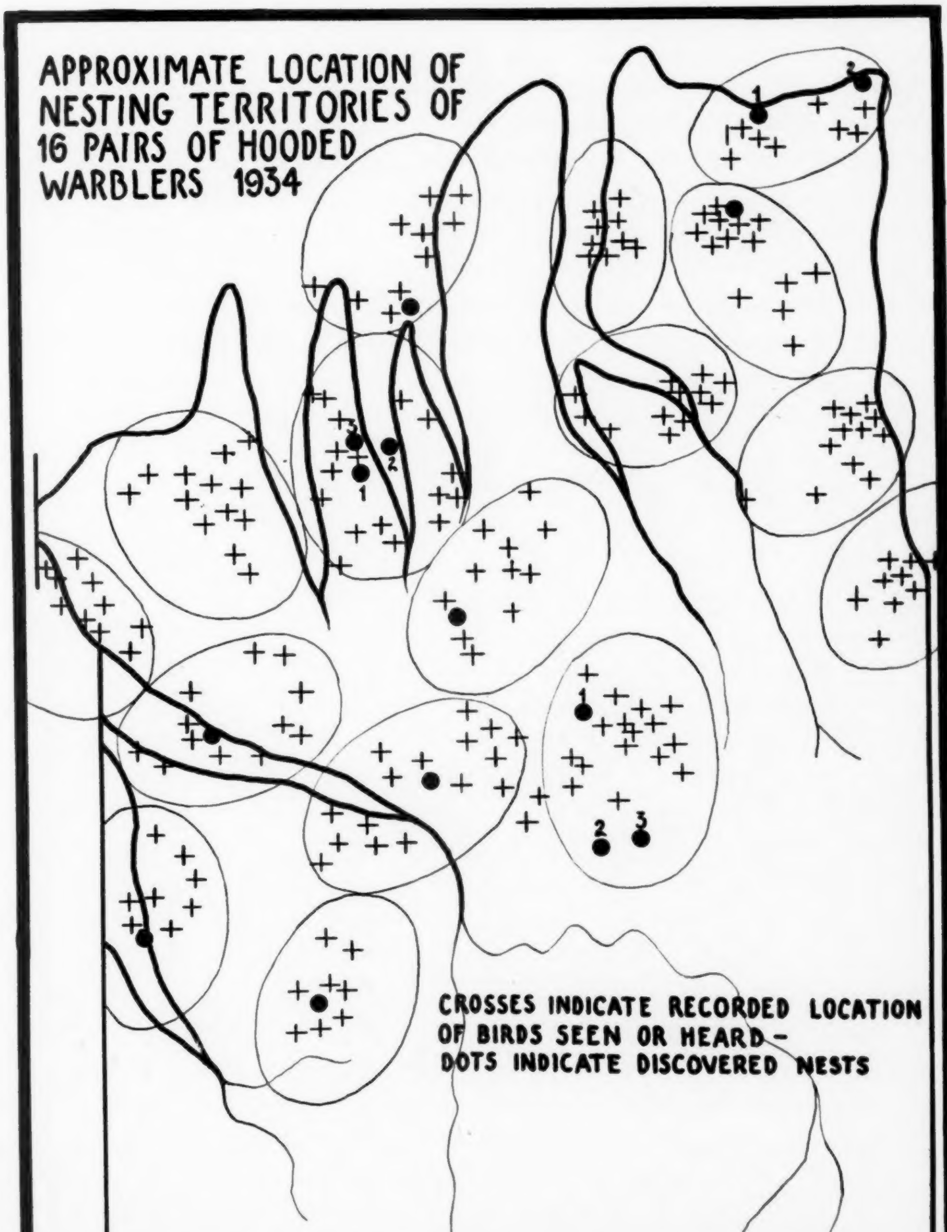

FIG. 14. Approximate nesting territories of hooded warblers in the area under study in 1934, on the basis of records made throughout the nesting season. First, second, and third nests of the same pair are numbered.

Schiermann (1930), studying the density of population of breeding birds in a forest in Brandenburg, Germany, adopted the method of laying out quadrats 250 meters (820.1 feet) square, and then searching systematically for every nest within the quadrat. From these sample quadrats the num-

ber of nesting pairs of birds in the whole area was then estimated. Schiermann found that his statistical results obtained from the quadrat agreed closely with figures arrived at from frequent visits to the area over a period of six years. He concludes, however, that his quadrats are of help only in conjunction with an intimate knowledge of the area obtained from long contact with it. With this conclusion the experience of the writer agrees.

The complete record of nesting birds in the area under study, as determined by the method of charting observed occurrences of the birds on a map, for the summers of 1932, 1933, 1934, and 1935 is shown in Table 17. Second and third attempts at nesting are not counted in this tabulation, but only the number of pairs of birds.

TABLE 17. Numbers of nesting pairs of birds.

Species	Numbers of Pairs			
	1932	1933	1934	1935
1. Red-eyed Viree	25	36	35	30
2. Wood Thrush	17	25	22	14
3. Hooded Warbler	15	15	16	9
4. American Redstart	12	17	19	19
5. Oven-bird	11	18	16	8
6. Tufted Titmouse	7	8	6	7
7. Black-capped Chickadee	6	5	3	2
8. Eastern Wood Pewee	6	7	7	7
9. Scarlet Tanager	6	6	10	9
10. Eastern Cardinal	5	5	5	4
11. Yellow-throated Vireo	4	4	7	3
12. Acadian Flycatcher	3	3	6	2
13. White-breasted Nuthatch	3	3	4	4
14. Black-throated Green Warbler	3	3	5	3
15. Red-eyed Towhee	3	1	2	1
16. Cerulean Warbler	2	2	1	0
17. Northern Downy Woodpecker	1	4	5	2
18. Eastern Hairy Woodpecker	1	3	3	3
19. Northern Crested Flycatcher	1	2	1	2
20. Eastern Phoebe	1	2	0	1
21. Northern Barred Owl	1	1	1	1
22. Eastern Robin	1	1	1	1
23. Louisiana Water Thrush	1	1	0	1
24. Northern Pileated Woodpecker	1	0	0	0
25. Northern Flicker	0	1	0	0
26. Rose-breasted Grosbeak	0	1	0	1
27. Red-bellied Woodpecker	0	0	1	0
28. Eastern Ruffed Grouse	?	0	0	0
29. Eastern Cowbird	*present*	*present*	*present*	*present*
Total pairs	136	174	176	134
Total individuals	272	348	352	268
Pairs per acre	2.0	2.6	2.7	2.0
Pairs per hectare	4.9	6.4	6.7	4.9
Average number pairs per acre, 4 years				2.3
Average number pairs per hectare, 4 years				5.7

It will be noted that the summer of 1933 showed a slight increase in numbers of nesting pairs, as contrasted with the great decrease in the mammal population of this period. The birds were unaffected by the failure of beech and sugar maple seeds, as these are not "basic" foods for them, as they are in the case of most of the mammals. They were also not affected by the dry weather of the summer so far as nesting activities were concerned, as the drought was most severe during late June, July, and August, when nesting activities were about over. If the bird population was affected by reduced numbers of insects following the drought, or if reproduction was cut down during the breeding season one would expect it to be reflected in the numbers of breeding pairs in 1934.

Figure 15 shows the approximate locations of the nesting sites of the 176 pairs of birds listed in Table 17 as having been recorded in 1934. As this figure is studied it should be kept in mind that we have here not only a horizontal distribution of nesting sites, but a vertical one as well, ranging from the tops of large trees, as in the case of the cerulean warbler, down through the various levels of forest growth to the nesting site of the ovenbird beneath the leaf-litter on the floor of the forest. Nesting territories may be separated from each other by distance vertically as well as by distance horizontally. The writer recalls one nest of the red-eyed vireo approximately 70 feet (21.3 meters) up, in a large beech tree, and another nest of the same species almost directly below it in a beech sapling about 6 feet (1.8 meters) from the ground. One vireo pair had a tree-top territory, the other almost a ground-level territory.

Using the breeding record as a basis for estimating the summer breeding population of birds, and the weekly counts of numbers observed at all seasons of the year, with due allowance for weather and other conditions affecting the counts, Table 18 has been prepared as an attempt to estimate the total bird population present at various times throughout the year. Only the fairly well-known species are included in this list as such. Others are totaled under appropriate headings. Young birds are not counted until they become independent of parents. While the figures are an attempt to approximate the highest population numbers reached each month even this figure is of course not constant during the month.

Food Chains and Ecological Niches

While the numbers of nesting pairs of birds in the area may at first glance seem to crowd the territory unduly, yet competition for food is really limited by reason of the territorial relations of competing species or individuals, and the particular ecological niches in the forest community occupied by others.

The barred owl, the ruffed grouse, and the robin probably do not com-

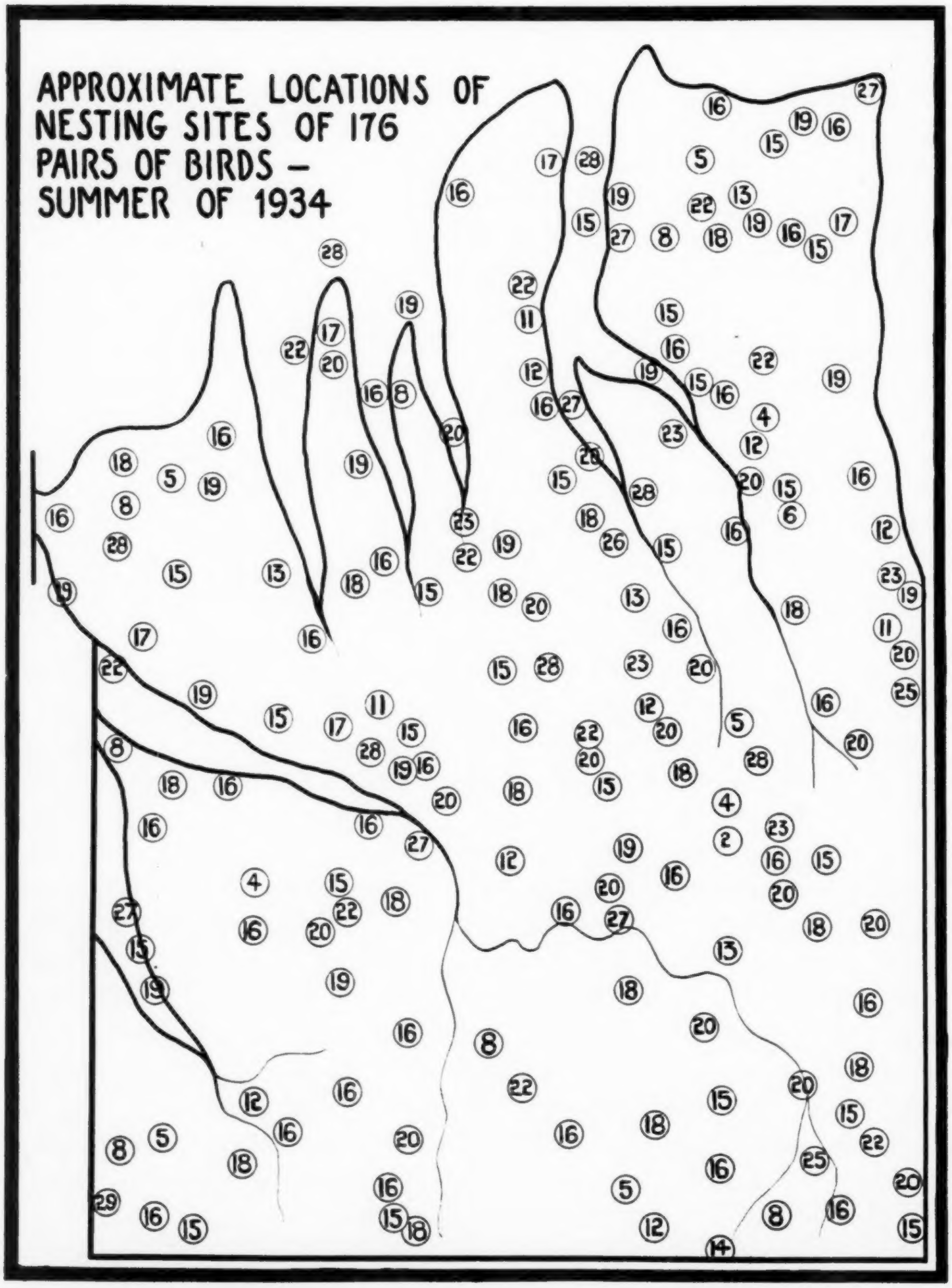

FIG. 15. Approximate locations of nesting sites of breeding birds in Table 17, summer of 1934.

2—Barred owl
4—Hairy woodpecker
5—Downy woodpecker
6—Crested flycatcher
8—Wood pewee
11—Chickadee
12—Tufted titmouse
13—White-breasted nuthatch
14—Robin
15—Wood thrush
16—Red-eyed vireo
17—Black-throated green warbler
18—Oven-bird
19—Hooded warbler
20—Redstart
22—Scarlet tanager
23—Cardinal
25—Towhee
26—Cerulean warbler
27—Acadian flycatcher
28—Yellow-throated vireo
29—Red-bellied woodpecker

TABLE 18. Estimated average bird population by months based on 1932, 1933, 1934, and 1935 figures.

	March	April	May	June	July	August	September	October	November	December	January	February
Permanent residents:												
Tufted Titmouse	20	20	14	14	12	12	12	20	20	20	20	20
Eastern Cardinal	10	10	10	10	10	10	10	10	10	10	10	10
White-breasted Nuthatch	16	16	10	6	6	6	12	12	30	20	16	16
Black-capped Chickadee	16	16	8	8	8	8	16	16	16	16	16	16
Northern Downy Woodpecker	16	16	8	6	6	6	10	10	16	16	16	16
Eastern Hairy Woodpecker	6	4	4	4	4	4	8	8	8	8	6	6
Red-eyed Towhee	10	10	10	4	4	4	4	4	10	10	10	10
Northern Barred Owl	2	2	2	2	2	2	2	2	2	2	2	2
Northern Pileated Woodpecker	2	2	2	0	0	0	2	2	2	2	2	2
Red-bellied Woodpecker	1	1	0	0	0	0	1	1	1	1	1	1
Eastern Ruffed Grouse	1	1	1	0	0	0	0	1	1	1	1	1
Totals	100	98	69	54	52	52	78	86	116	106	102	100
Summer residents:												
Red-eyed Vireo	...	...	82	62	50	30	20	...	...	...	...	...
Wood Thrush	...	...	54	38	32	20	10	2	...	...	...	...
American Redstart	...	...	50	34	16	8	...	...	...	...	...	...
Hooded Warbler	...	...	28	28	20	14	10	1	...	...	...	...
Oven-bird	...	...	40	26	14	8	6	5	...	...	...	...
Scarlet Tanager	...	...	16	16	12	8	4	...	...	...	...	...
Eastern Wood Pewee	...	...	10	14	14	10	6	...	...	...	...	...
Yellow-throated Vireo	...	...	10	8	6	2	2	...	...	...	...	...
Acadian Flycatcher	...	...	6	6	4	4	4	...	...	...	...	...
Black-throated Green Warbler	...	10	25	6	6	2	30	2	...	...	...	...
Eastern Cowbird	...	2	4	6	...	...	...	...	...	...	...	...
Cerulean Warbler	...	...	20	2	2	2	2	...	...	...	...	...
Northern Crested Flycatcher	...	...	4	2	2	2	1	...	...	...	...	...
Louisiana Water Thrush	...	4	10	2	2	2	...	...	...	...	...	...
Eastern Phoebe	...	...	4	2	2	2	...	...	...	...	...	...
Eastern Robin	...	6	2	2	2	10	100	500	250	2	2	2
Totals	...	22	365	254	184	124	195	510	250	2	2	2
Autumn and winter visitors, transients and occasionals												
Autumn and winter visitors	20	30	10	...	...	...	25	75	50	30	10	10
Red-breasted Nuthatch	20	40	15	...	...	...	10	60	75	50	30	25
Slate-colored Junco	50	50	...	...	...	...	...	50	50	25	10	5
Transient Warblers	...	10	300	...	...	15	150	50	...	...	...	...
Eastern Hermit Thrush	...	30	...	...	...	...	...	50	...	...	...	...
Olive-backed Thrush	...	...	75	...	...	...	50	75	...	...	...	...
Gray-cheeked Thrush	...	...	10	...	...	...	10	...	...	...	...	...
Wilson's Thrush	...	...	25	...	...	...	10	15	...	...	...	...
White-throated and Fox Sparrows	...	20	50	...	...	...	10	75	10	...	...	...
Occasional visitors	15	20	20	5	5	20	30	15	10	5	...	15
Totals	105	200	505	5	5	35	295	465	196	110	50	55
Grand Total	205	320	939	313	241	211	568	1061	562	218	154	157

pete with any other species for food. The woodpeckers, while all seeking their food in the same way, probably overlap very little, as the different species work upon different parts of the larger trees, and the downy pays a

good deal of attention to lesser growth, not worked by the other larger birds. While the 3 pairs of white-breasted nuthatches may sometimes come into competition with the downy woodpeckers, their nesting sites are widely separated so that competition is reduced to a minimum. The nuthatches may come into real competition with the chickadees and titmice, but this combination represents but 18 pairs of birds at its recorded maximum during the nesting season, which allows 3.6 acres (1.45 hectares) to the pair if the territory were evenly divided between them. As a matter of fact the chickadee and titmouse nesting territories seem to be complementary to each other, while the nuthatches cover a much wider range than either of the others.

So far as food habits are concerned the flycatchers form a group by themselves, each species having its own special hunting ground. The crested flycatcher pairs keep strictly to its part of the woods. The Acadians each have their own little glen, with a stream running through it, and no other flycatchers in the vicinity. The wood pewees have widely separated territories of their own in the higher levels of the forest. The hooded warblers and the redstarts may compete at times with each other, yet in a general way they are somewhat complementary as the redstart usually hunts in higher territory than does the hooded warbler.

The birds whose food habits call them frequently or almost entirely to the ground in summer—the Louisiana water thrush, oven-bird, wood thrush, cardinal, towhee—have about 2 acres (0.8 hectares) per pair on the average, which would furnish them with plenty of food supplies not drawn upon to any extent by other species.

This reserves the leafy foliage of the forest trees to the tanagers, vireos, and cerulean warblers—not entirely, of course, but this is their particular niche. The black-throated green warblers seem to keep pretty closely to the upper parts of the large hemlock trees during the nesting season, and their nesting sites are widely separated.

So far as factors within the environment are concerned this summer population of breeding birds seems to be regulated largely in its distribution and density within the area by the available food supplies, and the number and fitness of nesting sites and ecological niches offered by the forest environment.

It is difficult, if not impossible, to assign places of relative influence to particular species of birds inhabiting the community. In the aggregate the birds consume an immense amount of insect food as well as considerable vegetable matter. Certain groups, however, may be singled out as of outstanding importance because of numbers, or because of their constant activity throughout the year.

Probably the most influential of these groups is that composed of the

hairy and downy woodpeckers, chickadee, tufted titmouse, and white-breasted nuthatch. These are all permanent resident species, and their numbers are considerably increased at certain times of the year. They constitute a company of very diligent searchers after insects on and under the bark of trees, and in dead wood, dividing between them the territory to be covered, so that very little tree surface escapes their attention. Larvae of beetles and other insects, eggs, pupating insects, hibernating insects, spiders, myriapods, and others form the bulk of their diet. Beech nuts are eaten by all of these species as well as many wild fruits. Their limited range keeps them within the area, and thus entirely dependent upon it for their food supplies.

There is no doubt but that the heaviest summer influence is exercised by the group composed of wood thrush, oven-bird, hooded warbler, red-eyed vireo, redstart, and scarlet tanager. All these are highly insectivorous. They cover all levels from ground to tree-tops, and so serve as an efficient check to the summer insect population. Yet their stay in the area is limited, and their activities are spread over too short a space of time to give them first rank in influence. They supplement the activities of the first group when the insect tide is rising to its greatest proportions, and it may be questioned whether, in the absence of either group the forest could long continue to maintain itself. It is of interest to note how, in August, the chimney swifts and purple martins, hunting immediately above the forest roof, complete the occupation of all levels in the community of forest animals.

Another great bird group is that composed of robins, hermit thrushes, and olive-backed thrushes in autumn. Although these birds come mainly for forest fruits, among which the wild grape ranks high, they also spend much time raking over the dead leaves of the forest floor for insect food. Of great importance also is the frequently large group of migrating warblers in spring. Though their stay in the area is brief, they rid the developing foliage and bark surfaces of the trees of many newly hatched insects before the minuate larvae have developed into larger consumers of foliage.

The most important non-breeding bird in the area is the red-breasted nuthatch. Though present only in alternate winters during the period of this study, and though their numbers are marked by considerable fluctuation, they often surpass in numbers all other species put together. Their length of stay covers a period of over seven months, and while present they are apparently strictly resident. They are very diligent in their pursuit of food, spending much time searching the bark, limbs, twigs, and decayed places of the forest trees. Beech nuts are taken with evident relish. The red-breasts work all the way from the ground to the tops of the highest trees, and do not hesitate to enter the cavities of decaying logs.

The barred owl and the pileated woodpecker stand out because of their size and year-round activity. The woodpecker's range is much larger

than the area under study, and though a single pair, sometimes augmented by young in summer, or another presumably immature bird in winter, spend much time in the area, they are not dependent upon it for their living. Their work on hemlock trees infested by the bark-boring beetle is very evident. They also do much work in digging for grubs and ants in trees like the white ash, in which the heart-wood is decayed, but the sapwood is still sound. The pileated woodpecker is an influential bird in the area, but important in a supplementary way rather than primarily. On the other hand, the barred owl is more nearly resident, probably not going far beyond the limits of the area on his hunting trips. In summer the single pair of owls breeding in the beech-maple association seem to hold themselves and their young quite closely to the interior forest, appearing to be entirely dependent upon it for food supplies.

That short-tailed shrews form the bulk of the owl's diet is very apparent. The barred owl has frequently been observed in the act of catching these little animals, and no cast pellet so far examined has failed to include jaws or skulls of from 1 to 4 shrews *(Blarina brevicauda)*. Remains of the white-footed mouse are also frequently found, but not always, as is the case with the shrew. Though these two animals probably make up most of the barred owl's diet, the writer is inclined to the opinion that a considerable number of the smaller insectivorous birds are also consumed, especially in early spring when the summer resident bird population is concentrating its activities upon the incubation of eggs and rearing of young. The frequently deserted and destroyed nests found at this season strongly suggest that the incubating or brooding bird has come within range of the owl's telescopic vision, and has been picked off—sometimes nest and all. When the owl's nesting site was examined in April 1932, after the young had come off, feathers of hairy woodpecker, red-bellied woodpecker, blue jay, cedar waxwing (*Bombycilla cedrorum* Vieillot), bob-white, and horned lark (*Otocoris alpestris* Linn.) were recovered from the débris at the bottom of the nesting cavity. The presence of horned lark feathers certainly indicates an excursion into the open fields outside the woods, and the bob-white and cedar waxwing remains are corroborative evidence of the same thing. The barred owl therefore is of large importance in the community as a check upon the numbers of shrews and mice, and to a much less extent as a limiting influence on the reproduction of smaller birds within the area.

It is more difficult to classify the birds of the area on the basis of food habits than it is the mammals. The barred owl is the only one among the permanent residents to be classed as a carnivore. Yet he is also an eater of insects (Fisher 1880). The other permanent residents, while all consuming considerable vegetable matter, particularly beech nuts, could probably, with the possible exception of the ruffed grouse, get along quite well in

the absence of vegetable provender. The summer residents are predominantly insectivorous—the flycatchers, warblers, vireos, and tanager completely so (Forbush 1927, 1929). Thus it appears that the bird population of the area, with the exception of the barred owl, is supported mainly by the insect food supplies of the forest, and only secondarily, and to a much less extent, by plant products.

Seasonal Changes in the Bird Population of the Area

One of the main characteristics of the bird population of the area under study is its instability. Fluctuations in numbers are at times extreme, and even in winter numbers are far from constant. While the total of species listed is 83 (Table 16), only 11 of these are classed as permanent residents. Even the summer nesting species constitute a rapidly shifting element in the total bird population. What the increase in numbers may be when young birds are launched upon independent careers is largely a matter of conjecture, for it is certain that most of the summer resident species leave the area with their young as soon as the latter are capable of sustained flight. One must also allow for a large mortality among both young and old, and must count upon a large percentage of failures of nesting pairs to bring any young birds off the nest. Butts (1930), working with banded white-breasted nuthatches, noted the frequent disappearance of apparently permanent resident birds. Out of 21 individuals, 10 disappeared in two years, and only one, banded at the beginning of his study, lasted throughout the three years of its duration. Probably the length of life of most small birds is not more than two years on the average. The probability is that when the summer is over, the net increase in the bird population is not large. Depletions from the ranks of the older birds are made good by the entrance of younger birds into the community, perhaps in numbers just large enough to absorb the losses that are due to come as a result of autumn and winter casualties, and so maintain the species at about its normal numbers.

Reference to Table 18 will give an idea of constantly changing numbers, but when this is reduced to diagrammatic form (Fig. 16) the often extreme and abrupt fluctuations as well as the more gradual changes in the bird population of the area are clearly apparent. As the red-breasted nuthatch has been present only on alternate years, this species is set off from the other winter visitors.

It is in the spring and autumn that the fluctuations in number of birds in the area are relatively enormous. During the first half of the month of May the woods are flooded with migrant species on their way to more northerly breeding grounds. At the same time the greater number of the summer resident species are arriving. In October and November the woods are again filled with large numbers of robins and flocks of migrating thrushes

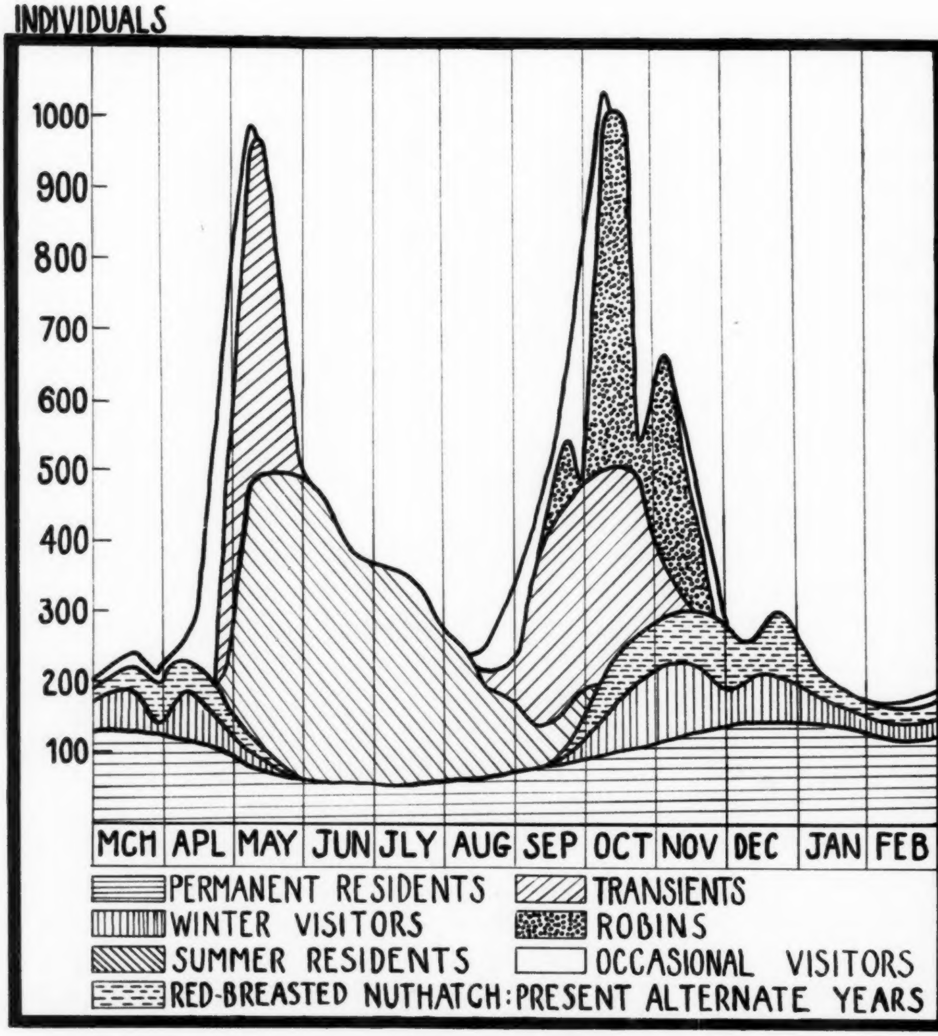

FIG. 16. Seasonal fluctuations in the bird population of the area under study on the basis of estimates and averages of weekly counts for 1932, 1933, and 1934.

and sparrows. The winter visitors are already well massed in October and reach a peak of numbers in November. These two months witness the largest assemblage of birds in the area during the year. The two periods of least numbers are the second week in August, when the summer population is depleted, and the last week in January, when many of the winter visitors have left the area and the influence of the northward movement is so soon to come is not yet evident.

THE REPTILES OF THE AREA

During the first two and a half years of this study the only reptiles observed in the area were snakes. In the spring of 1934 Mr. M. B. Walters

and the writer together were fortunate enough to get very good sight records of several five-lined skinks, thus adding a lizard to the list. The reptiles thus far observed, specimens of all of which except the skink have been collected, are shown in Table 19. Scientific names are as used by Ditmars (1920).

TABLE 19. Reptiles of the area.

Five-lined Skink	*Eumeces quinquelineatus* (Linn.).
Ribbon Snake	*Eutaenia saurita* (Linn.).
Common Garter Snake	*Eutaenia sirtalis* (Linn.).
Common Water Snake	*Tropidonotus fasciatus sipedon* (Linn.).
De Kay's Snake	*Storeria dekayi* (Holbrook).
Red-bellied Snake	*Storeria occipitomaculata* (Storer).
Pilot Blacksnake	*Coluber obsoletus* (Say).
Milk Snake	*Ophibolus doliatus triangulus* (Daudin).

The skinks were observed on May 7, 1934, running in and out from under the loose bark on a large fallen beech log, evidently enjoying the brilliant spring sunshine which was a feature of that day. Three were seen at one time and two at another, but the total number may not have been more than three. One of these was in the "blue-tailed" stage, the others brown, with characteristic red heads. As this is the only recorded occurrence of these animals in the area their numbers must be few.

The common garter snake and the ribbon snake, while regularly found, are not abundant. Five small immature common water snakes have been taken in or near the course of the main stream bed in the area. This species is common in a pond about a half mile west of the area, and these young snakes may possibly have come into the woods from that direction. Three specimens only of the milk snake have been taken. Five fine examples of the red-bellied snake have been found, one of which, while in temporary captivity, gave birth to 21 living young. The period of activity of these snakes is from about May 1 to the latter part of October.

The only reptile inhabiting the area that can be said to be present in numbers is the pilot blacksnake. During the summer of 1931 12 or 13 of these beautiful serpents were taken in the area. Most of these were over 4 feet (121.9 cm.) in length; several were over 5 feet (152.4 cm.); and the cast "skin" of one has been found measuring 6 feet 1 inch (185.3 cm).

After several days in captivity the pilot blacksnake can be handled easily. Captive specimens have proved to be remarkably expert in climbing, and exceedingly muscular in action. According to Ditmars (1920), the snakes of the genus *Coluber*, to which the pilot blacksnake belongs, feed upon warm-blooded prey exclusively—especially the smaller rodents—and also upon birds and their eggs. One is mentioned as having disgorged a well-grown cottontail rabbit upon being captured. Captive snakes of this species, observed by the writer, took three young scarlet tanagers which were found dead, their nest having been blown down in a storm. One was reported as

having been seen coiled about a wood thrush's nest some 20 feet (6 meters) above the ground in a young sugar maple sapling, having apparently made a meal of the young birds.

When released, these snakes quickly disappear beneath the leaf litter, or into any near-by cavity under a log or stump. One can easily see what an efficient hunter of chipmunks, mice, shrews, and young birds an animal of this sort might be.

The earliest record of the appearance of the pilot blacksnake in spring in the area is May 2. On this date the writer saw a fine specimen which when measured later proved to be 4.5 feet (137.1 cm.) in length. There was considerable soil adhering to the reptile's back, as though he might have just emerged from an underground retreat. He was lethargic, allowing the camera tripod to be set up within a few inches of his head, and when picked up showed no signs of fight, which is unusual in this species. The inference was that he had just emerged from hibernation. As these snakes disappear in October, this allows for a full six months period of activity.

As to the rate of reproduction of the pilot blacksnake, one captive specimen, 5 feet 4 inches (162.5 cm.) long deposited 22 eggs on July 18. Several days later, another of lesser length laid 13 eggs.

The pilot blacksnake is well distributed throughout the area, having been observed in all parts of it, including beech-hemlock environment. During the past three years 10 of these snakes have been marked by making a deep V-shaped nick in the outer edge of one of the ventral plates, and then have been set at liberty. The number of the marked plate, counting from the anus has been recorded in each case, being a different number for each snake. One of these, marked in the summer of 1932, was recovered near the point of original capture and set at liberty again May 6, 1934. This would seem to indicate a rather closely resident character for these serpents. The numbers of pilot blacksnakes, judging from captures made, seemed to be fairly constant in 1932 and 1933, but were distinctly less in 1934 and 1935. This is apparently correlated with the falling off in numbers of small mammals in 1933 and 1934.

The importance of the garter snake, ribbon snake, and water snake in the area seems relatively very small because of their insignificant numbers, small size, and food habits which restrict them to insects, worms, frogs, and toads. If the milk snake should be found here in numbers, it would need to be classed as an important member of the community, but at present there is no evidence that this is the case. The red-bellied and De Kay's snakes may be present in greater numbers than the few records indicate. They are secretive in habits, and normally not often seen. Ditmars (1920) says that the food of these snakes consists of earthworms, slugs, and the soft-bodied grubs of beetles. Their burrowing habits might make them

important insect hunters in decaying stubs and logs. If present in numbers they would therefore be important members of the forest community.

The pilot blacksnake must be classed as among the really important members of the community. In size, in numbers, in food habits, in rate of reproduction, and in activity it ranks well up among the more important animals of the area.

THE AMPHIBIA OF THE AREA

The list of amphibians thus far discovered in the area is shown in Table 20.

TABLE 20. Amphibia of the area.

Toads and frogs	
American Toad	*Bufo americanus* Le Conte.
Fowler's Toad	*Bufo fowleri* Putnam.
Pickering's Hyla	*Hyla crucifer* Wied.
Green Frog	*Rana clamitans* Latreille.
Eastern Wood Frog	*Rana sylvatica* Le Conte.
Salamanders	
Brown Salamander	*Desmognathus ochrophaea* Cope.
Dusky Salamander	*Desmognathus fusca* (Rafinesque).
Spotted Salamander	*Ambystoma punctatum* (Linn.).
Mole Salamander	*Ambystoma talpoideum* (Holbrook).
Red-backed Salamander	*Plethodon cinereus* (Green).
Slimy Salamander	*Plethodon glutinosus* (Green).
Red Eft	*Triturus viridescens* Rafinesque.

Toads and frogs are not abundant in this forest community. But 3 records of the American toad, and 5 of Fowler's toad have been made. The wood frog and Pickering's hyla occur more frequently but have never been observed in numbers. Each is generally distributed throughout the area, but more often encountered on the lower levels than on the higher land. During the summers of 1931 and 1932 the green frog was the common frog of the area. Nearly every pool of standing water had its one or more small half-grown frog of this species. During dry weather they would disappear, but after a rain would appear again. In 1933 green frogs were scarce in the area, and in 1934 and 1935 they were completely absent. After the dry summer of 1933 all frogs became exceedingly scarce in the area.

Nor are salamanders abundant. The commonest species is *Triturus viridescens* in the second larval form commonly known as the "red eft." The adult form is very common in a pond to the west of the area. After a rain in summer these brilliant red salamanders may be seen walking abroad quite fearlessly. The writer has seen both the raccoon and the crow refuse to eat the red eft, though they would take salamanders of other species. Perhaps this matter of being unpalatable may account for the somewhat greater abundance and lack of fear of this species. The dusky salamander is quite abundant in certain wet places under stones in stream beds. The red-backed and brown salamanders are both found sparingly under logs and bark or in moist dead wood. The slimy salamander seems to be

rather generally distributed through both associations, but quite sparingly, while the spotted salamander and the mole salamander are rare. After the very dry summer of 1933 all salamanders became quite rare in the area, the red eft being the only species that seems to have escaped a drastic reduction in numbers.

Not much can be said at this time as to the relative importance of amphibia in the area. That frogs are an item in the fare of the raccoon may be infered from the abundance of the raccoon tracks about the places where frogs are to be found. Doubtless most of the other amphibians, when encountered, would be added to the raccoon's diet. The same would hold true for the skunk and the opossum, and doubtless for other mammals and some birds. The ribbon snake, the garter snake, and the water snake are known to be addicted to amphibian fare (Ditmars 1920).

On the other hand the toads, frogs, and salamanders fill a definite niche in the economy of the forest as large consumers of insects, slugs, and larvae. Yet because of their small numbers in the area under study they do not seem to be of great importance to the community as a whole.

INVERTEBRATES OF THE AREA

The molluscs listed in Table 21 have all been collected as live animals within the area and the dead shells of many of them are quite common on chipmunk feeding tables and in shrew runways.

TABLE 21. Molluscs of the area.

Polygyra stenotrema (Ferussac).	*Polygyra fraterna* (Say).
Polygyra tridentata (Say).	*Omphalina inornata* (Say).
Polygyra fraudulenta (Pilsb.).	*Omphalina fuliginosa* (Griffith)
Polygyra albolabris (Say).	*Anguispira alternata* (Say).
Polygyra albolabris dentata Tyron.	*Succinea retusa* Lea.
Polygyra thyroides (Say).	*Succinea ovalis* Say.
Polygyra clausa (Say).	*Circinaria concava* (Say).
Polygyra zaleta (Binney).	*Vitrea hammonis* (Ström.)
Polygyra palliata (Say).	*Zonitoides minuscula* (Binney).
Polygyra hirsuta (Say).	*Limax maximus* Linnaeus.

Cahn and Kemp (1929) mention finding the shells of *Anguispira alternata* and *Polygyra stenotrema* in nests of the white-footed mouse. Shull (1907) found that in winter, snails of the genus *Polygyra (albolabris, multilineata, profunda, thyroides, fraterna)* formed much of the food supply of the short-tailed shrew. That land snails are preyed upon by certain beetles and their larvae is also established (Lengerken 1934, Boettger 1934). Boycott (1934) says that competition between land snails is an almost negligible factor, and that there is no specific relation between Mollusca and trees.

The crayfish *Cambarus bartoni robustus* Girard is common in the main stream bed of the area. Crayfish are said to be fed upon by raccoons, salamanders, frogs, birds, snakes, turtles, and fishes (Turner 1926). The same

author says that crayfish are generally omnivorous, eating almost anything of an organic nature that comes to hand, whether of animal or vegetable material.

The temporary pools in the beech-maple association were studied in the spring of 1933 by Dr. Norma C. Furtos. During this study the temperature of the water varied from 40° C. (39.2° F.) on April 8 to 15° C. (59.° F.) on April 28. Organisms found are listed in Table 22.

TABLE 22. Organisms in temporary pools.

Arcella sp.	*Candona decora* Furtos.
Trachelomonas sp.	*Candona brevis* Muller.
	Eucypris sp.
Planaria velata Stringer. (common)	*Eucypris fuscata* (Jurine) var. *gigantea* Furtos.
Alona guttata.	*Eucypris* sp.
Chydorus sphaericus (O. P. Müller).	*Cypricercus tincta* Furtos.
Cyclops viridis Jurine.	*Cryptocandona* sp.
Cyclops crassicaudis Sars.	
Cyclops serrulatus Fischer.	*Gammarus* sp.
Cyclops bicuspidatus Claus.	*Eucrangonyx* Sp.
Canthocamptus staphylinoides (Jurine).	*Macrobiotus* sp.

In addition to the species listed (Table 22) aquatic earthworms were commonly found, a small crayfish was taken, and larvae of caddis fly, may-fly, *Diptera* and *Coleoptera*, were found to be common. Mosquito larvae were very abundant. Red water mites were common.

Obviously no complete understanding of the dynamics of the forest can be secured without a thorough study of its insect life. This should be done quantitatively as well as qualitatively. On all sides the evidences of the activities of wood-boring and bark-boring insects are apparent. There are bees and flies and wasps and butterflies and small midges and mosquitoes in the air. Moths large and small are common. The big syrphid fly *Milesia virginiensis* Dru. is common, as are the scavenger beetles *Necrophorus marginatus* Fab. Camel crickets are abundant in the humus in certain places. Ground beetles are abundant everywhere. The yellow-jacket *Vespa communis* De S. and the white-faced hornet *Vespula maculata* (Linn.) are very common. The writer counted 9 large nests of the latter species in the winter of 1934-35 in the area. The work of the flat-headed hemlock borer *Melanophila fulvoguttata* Harr. is very noticeable in the beech-hemlock areas. The fungi of the area support a numerous insect population. In September the white woolly aphid *Schizoneura imbricator* Fitch. is often noted on the branches of the beech. Various kinds of caterpillers are noted on the foliage of the trees, and vireos and warblers seem to find much to glean from foliage beyond the range of one's vision. In August and September the hum of insects is a definite feature of the forest.

By reason of their numbers, their destructive activities from the standpoint of plant life, their rôle as reducing agents in dead and decaying tim-

ber, their interrelations within their own group, their relations to other animals as parasites, and their great importance as a source of food supply, insects occupy a place of great significance in the biotic community. While their importance is recognized, it is impossible here to do more than call attention to it.

ECOLOGICAL CLASSIFICATION OF ANIMALS

The study of animal ecology has not as yet developed a commonly accepted terminology. As that suggested by Smith (1928) does not seem to the writer to be entirely adequate to some of the situations arising in this study, the following special terms are herein employed:

1. Predominants are those animals which are most abundant in numbers and of greatest influence in the community.

2. Members are those animals that are present in smaller numbers than predominants, and therefore of lesser influence. The term may be applied to a single individual.

Both predominants and members may be further subdivided by employing the following adjectives.

1. Permanent. Used to indicate constant presence and activity throughout the year.

2. Fluctuating. Used to indicate marked lack of constancy in numbers and activity at different seasons, although present throughout the year.

3. Seasonal. Used to indicate presence or activity at one or more seasons of the year and entire absence or inactivity at others.

4. Incidental. Used to indicate irregular and inconsequential occurrence in the community.

TABLE 23. Ecological classification of vertebrates in the beech-maple association.

Predominants	Members
Permanent predominants	Permanent members
Mammals	Mammals
Short-tailed Shrew	Eastern Red Fox
Northern White-footed Mouse	New York Weasel
	Southern Red Squirrel
	Small Eastern Flying Squirrel
	Domestic Dog
	Domestic Cat
Birds	Birds
Eastern Hairy Woodpecker	Eastern Ruffed Grouse
Northern Downy Woodpecker	Northern Barred Owl
Black-capped Chickadee	Northern Pileated Woodpecker
Tufted Titmouse	Red-bellied Woodpecker
White-breasted Nuthatch	Eastern Cardinal
Fluctuating predominants	Fluctuating members
Mammals	Mammals
Northern Gray Squirrel	Cottontail Rabbit
Eastern Chipmunk	Smoky Shrew
Pine Mouse	
Birds	Birds
Eastern Robin	none

Seasonal predominants

Mammals

none

Birds

(nesting species

Red-eyed Vireo
Wood Thrush
Hooded Warbler
American Redstart
Oven-bird
Eastern Wood Pewee
Scarlet Tanager

(transient species)

Eastern Hermit Thrush
Olive-backed Thrush

(winter resident species)

Red-breasted Nuthatch

Reptiles

Pilot Blacksnake

Amphibians

Green Frog
Wood Frog
Pickering's Hyla

Red Eft
Red-backed Salamander

Seasonal members

Mammals

Virginia Opossum
Eastern Raccoon
Eastern Skunk
Southern Woodchuck
Big Brown Bat

Birds

(nesting species)

Crested Flycaster
Acadian Flycaster
Eastern Phoebe
Yellow-throated Vireo
Cerulean Warbler
Louisiana Water Thrush
Rose-breasted Grosbeak
Red-eyed Towhee

(transient series)

American Woodcock
Yellow-bellied Flycatcher
Winter Wren
Gray-cheeked Thrush
Wilson's Thrush
Eastern Golden-crowned Kinglet
Eastern Ruby-crowned Kinglet
Blue-headed Vireo
Black and White Warbler
Blue-winged Warbler
Nashville Warbler
Magnolia Warbler
Black-throated Blue Warbler
Blackburnian Warbler
Chestnut-sided Warbler
Blackpoll Warbler
Connecticut Warbler
Canada Warbler
Purple Finch
White-throated Sparrow
Fox Sparrow
Yellow-bellied Sapsucker

(winter resident species)

Eastern Goldfinch

Reptiles

Five-lined Skink
Ribbon Snake
Garter Snake
Red-bellied Snake
De Kay's Snake
Milk Snake

Amphibians

American Toad
Fowler's Toad

Dusky Salamander
Brown Salamander
Slimy Salamander

Incidental Members

Mammals

Fox Squirrel
Meadow Mouse
Star-nosed Mole
Hairy-tailed Mole
Red Bat
Silver-haired Bat

Birds

Turkey Vulture	Chimney Swift	Eastern Blue Grosbeak
Sharp-shinned Hawk	Ruby-throated Hummingbird	Indigo Bunting
Cooper's Hawk	Northern Flicker	Common Redpoll
Eastern Red-tailed Hawk	Northern Blue Jay	Red Crossbill
Broad-winged Hawk	Purple Martin	Slate-colored Junco
Eastern Bob-white	Eastern Crow	Eastern Whip-poor-will
Eastern Mourning Dove	Starling	Reptiles
Yellow-billed Cuckoo	Brown Creeper	Common Water Snake
Great Horned Owl	Carolina Wren	Amphibians
Eastern House Wren	Bronzed Grackle	Spotted Salamander
Eastern Nighthawk	Eastern Cowbird	Mole Salamander

ASPECTION

Aspection, or phenology, has to do with the visible evidence of the responses which plants and animals make to the changing of the seasons. It is usual to divide the year on the basis of plant activity into six main periods, or aspects; the prevernal, vernal, aestival, serotinal, autumnal, and hibernal (McDougall 1927, Weaver and Clements 1929). While this has been adopted also for animals as a convenient way of designating seasonal changes, it is difficult to assign time limits to any of these divisions since one merges insensibly into another. In discussing fluctuations in abundance of mammals, birds, and other animals in the community under study, reference has been made to certain seasonal changes in numbers. These also constitute parts of seasonal aspects.

The main changes to be noted in the aspect of the forest composing the beech-maple association at North Chagrin are somewhat as follows:

1. *Prevernal aspect.* Although February is usually the coldest month of the year (Fig. 3) and most of its aspects are hibernal, yet in this month mosses and lichens definitely take on new color, and during the latter part of the month, crows and hawks appear. Tufted titmice and cardinals begin to whistle occasional spring-like notes, and the pileated woodpecker becomes noisy. The woods are very wet from melting snow or rains, and standing water in pools is a feature of the aspect.

By the first week in March some of the plants that have carried green leaves over winter, like spring cress and wild blue phlox, or some of the violets, show definite responses in the erection of their stems and leaves, while the green leaves of wintergreen, partridgeberry and trailing arbutus take on new freshness. Although there is much alternation of freezing and thawing during the month the development of herbaceous vegetation is only temporarily checked by low temperatures, and responds rapidly to increasing warmth. Beech nuts and sugar maple seeds sprout in March even though they are bound to be covered with snow or encased in ice before the month is out.

By the latter part of March hepaticas and spring beauties may be found

in bloom—the hepaticas on certain south-facing slopes, and the spring beauties on the less wet places of the higher portions of the area. Certain species of mosses and lichens will be developing their fruiting bodies. *Protococcus* on beech trunks, and the green alga of the temporary pools start new growth. Throughout the month the barred owl has been sitting on her eggs, and both skunk and woodchuck have come out of hibernation. The tracks of raccoons have become common, chipmunks appear in numbers, bird music increases, and woodpeckers indulge in much drumming.

Unless delayed by snow or unduly low temperatures a great change takes place in the aspect of the forest during the latter part of March and the first of April. The higher land begins to green with the developing leaves of yellow adder's tongue, cut-leaved dentaria, and spring cress. Many plants of spring beauty come into bloom but they do not add appreciably to the green of the forest floor as the color of their leaves is more red than green. Many other plants are now recognizable. The spikes of both red and white trillium are emerging, rue anemone is in the "grape" stage, sweet cicely, Canada violet, blue cohosh, early meadow rue, golden seal, wild leek, wild blue phlox, swamp buttercup, and dutchman's breeches may all be recognized by the practiced eye. The heart-shaped cotyledons of seedling jewelweed are thickly scattered in certain locations. Many clumps of hepatica in bloom may be seen in favorable situations. The flower buds of elms and red maples are large and swollen, and gray squirrels begin to cut them down for food. The voice of *Hyla crucifer* is added to the early spring bird music. On the lower levels near the ground are many insects, particularly mosquitoes, small flies, small bees, and larger honey bees. Mourning cloak, question mark, and red admiral butterflies may be seen. The winter bird companies begin to break up.

By the second week in April the greening of the forest floor has progressed considerably. The foliage of spring beauty, spring cress, cut-leaved dentaria, dutchman's breeches, hepatica, and other plants has now definitely occupied the ground. This is the beginning of the "wildflower" display. From April 10 to 15 hepaticas will be at the height of their blooming season, and so quickly does the peak of their blossoming time pass, that one of these days will stand out above others for the abundant display that it offers. Spring beauties will begin to occupy the ground with their pink and white blossoms a few days later. Both these plants close their flower-heads on overcast, rainy, or cloudy days, so that their color pattern on the forest floor may be withdrawn at times. If snow comes, their flowers or leaves will often be seen protruding from the surface of the white blanket. The woods are still wet at this time of year, and standing water continues in the surface pools.

The buds of the forest trees are swelling now and so adding a new note

of color to the upper stories of the woods. Red-berried elder is sprouting vigorously. Fly honeysuckle comes into bloom. The leaves of wild black cherry break from the buds. The round-leaved violet comes into bloom, the flowers appearing before the leaves.

Titmice are constantly calling and woodpeckers drumming. The first of the summer resident birds—the phoebe—may be found about the wet places where insects are on the wing. The temporary pools swarm with minute forms of plant and animal life. As increasingly more sunlight reaches the forest floor through the leafless branches of the trees, differences in humidity as between day and night often become extreme. By the latter part of April yellow adder's tongue reaches a climax of bloom so that certain places are suffused with its yellow color. Red trilliums are now at their best, and some white trilliums are blossoming. Leaves of May apple begin to be noticeable. The breaking of the leaf buds on the trees gives the branches a filmy appearance and the sky begins to be shut out a bit.

The first week in May marks the high tide of the wild-flower display in the beech-maple association. The great white trillium now occupies the center of the stage and many of the less numerous species are in bloom. Spring beauty spreads itself like a pink carpet on the higher lands. The forest floor seems to be fully occupied with herbaceous growth, and sprouting seedlings of beech and sugar maple are recognized by their cotyledons. The buds on the forest trees now begin to break, and on a certain day the air will be filled with the falling bud-scales of beech. When viewed from a distance these opening buds give characteristic color to the forest trees. Brown indicates beech; green, sugar maple; and red, red maple. Both the beech and the sugar maple now come into bloom—the blossoms of the sugar maple imparting to the trees a brilliant yellow-green color in sunlight. Gray squirrels will be noted in the tree tops feeding upon beech blossoms.

This is the time when the summer resident birds appear, and when the woods may be flooded with warblers and other transient species. On the newly developing foliage tiny caterpillars appear, and in the air there is a surge of newly awakened insect life. Permanent resident birds are already nesting.

In the beech-hemlock association the Canada mayflower is the only herbaceous plant that forms a ground cover. Spikes of this plant appear in late April and the flowers begin to open about May 15.

2. *Vernal aspect.* The aspect of the forest is now rapidly changing, due to the unfurling of the leaves on the trees. Those on the lower levels are the first to expand, making a story of green below the tree tops. About the 10th or 11th of May occurs a day when the trees are hazy with the yellow-greens of newly unfolding leaves. During the time of leaf development on the trees the great white trilliums begin to turn pink and then to fade. As

they pass, the floor of the woods again takes on a yellow hue as three species of yellow violets come into their full flowering season. After them comes the time of flowering of wild blue phlox and wild geranium, but these plants are not in sufficient numbers to add much color to the picture. Seedlings of sugar maple and beech now contribute a good deal of green to the floor of the forest as the earlier herbaceous plants disappear. The green of new leaves of hepatica and May apple also add to the green mantle. From now on the flowers of the herbaceous vegetation are of the more inconspicuous types. The elms and the red maples have already shed their seeds.

As the leaves on the larger trees of the forest develop, less and less blue sky can be seen, until there arrives a time in the latter part of May when the fully expanded leaves shut out the sunlight altogether. The woods are now dark, even at mid-day. This is the time when the spring chorus of the chipmunk reaches its crescendo. These animals are very much in evidence as the dense curtain of foliage shuts the arboreal squirrels from view. The poikilotherms—pilot blacksnake, frogs, toads, salamanders, and snails—are now noticeable. The month of May also witnesses the great northward flight of the transient bird group. Warblers will be noted in the woods, and sparrows under the grape tangles and other débris. It is during the first two weeks of May that the summer resident birds are occupying their breeding territories. The woods are vocal now with bird songs. Insects become abundant. The Acadian flycatcher and the wood pewee complete the list of the summer residents. Now comes the great period of nest building and incubation of eggs. The barred owl, nesting earliest of all, has brought off her brood of three young by the last of April, and now they may frequently be located in the twilight as they beg for food. Young hairy woodpeckers become noisy in their nest holes.

May and June are periods of intense activity among the birds of the area and everything seems to be tense with the pressure of the advance of the season. Both permanent and summer resident species, having appropriated their share of the available nesting territory, are absorbed in the task of reproduction and the placing of their young upon a semi-independent footing in the community. Population density of breeding birds and mammals is at its maximum by the middle of June. Territory lines have been strictly drawn until now, but are relaxed as the summer resident birds bring their young off the nests. This change has already taken place in the case of most, if not all, of the permanent residents. Young gray squirrels, red squirrels, and chipmunks are very noticeable. All hibernators are active and migration is at a standstill. Food is abundant, and the amount of insects consumed must be enormous. Predators, with their own young to provide for, are very active. On days when the humidity is high, frogs, salamanders, snails, and slugs may be found. But this climax of activity quickly passes.

Mortality of young is high, and the moving of the summer bird population out of the area begins quickly.

3. *Aestival aspect.* By the 20th of June a change in activities is noticeable, particularly as regards the bird population, as the summer residents begin to move. Of these the redstart is the most hurried in its departure, young and old quitting the area by the end of June, after a stay of but a little over 60 days. A few redstarts will be seen later but these are probably transients or delayed nesters. The oven-birds follow closely upon the heels of the redstarts. The first week in July sees them practically gone. By the end of July the red-eyed vireo and the wood thrush have moved out. Certain pairs of birds, unsuccessful in the first attempt to raise a family, persist through three, or even more trials, thus prolonging the stay of a small portion of their group through July, or even longer. But by August most of the summer residents have gone.

By mid-June many bird songs are shortened or greatly modified, and many species have become quite silent. This is often a period of dry weather. The pools dry up, the withered plants of May apple and cut-leaved dentaria lie yellow and prostrate upon the ground, the green carpet of May is replaced by one of rich brown as the dead leaves of last autumn are exposed except where seedling beeches and maples have taken their stand. What vegetation of herbaceous character remains begins to look tattered and shopworn. Forest fruits are developing and squirrels are already cutting down the unripe beech nuts, hickory nuts, and acrons. Tupelo is shedding some scarlet leaves. The round-leaved green orchid and the nodding pogonia belong to the aestival aspect of the forest as they come into bloom at this time. Purple martins and chimney swifts, hunting above the forest roof, now testify to the fact that insects are flying overhead in the sunshine. Tufted titmice may be observed shepherding their families noisily about. A cardinal's tail feather on the ground suggests that this is the period of moulting and aestivation, and shortly chipmunks disappear into their underground quarters. Temperatures are high, the cicadas are noisy, "punkies" *(Culicoides)* become very annoying to humans.

4. *Serotinal aspect.* From mid-August to late September the forest seems silent and deserted. Nesting territories are now disregarded and there is apparent a tendency for birds to travel together in groups. Wandering families of nuthatches, titmice, and chickadees are encountered. If there are moist places in the woods the woodcock is liable to be found here. Nests of the paper wasp have now assumed large proportions. As the fruits of tupelo, hemlock, cucumber, and the oaks develop they are prematurely gathered by blue jays, gray squirrels, red squirrels, and chipmunks. Not only is there an immense amount of fruiting and seeding of forest trees, but also of herbaceous plants. Mushrooms become a feature of the aspect, often in

brilliant colors, and miniature forests of beech drops occupy large spaces about the bases of the beeches. Again the chipmunks, now emerging from their period of aestivation, yield to the ecstasy of the spring chorus. The first migrant birds of autumn—certain warblers, and later, the brown creeper and the golden-crowned kinglet—appear. Black-throated green warblers become briefly abundant beyond the numbers of the summer residents as the southward movement of the species as a whole begins. An inspection of Figure 16 will show that this is a period of low bird population numbers with the flow of bird life constricted into a narrow channel. But in September the stream widens and a period of great unrest is ushered in.

5. *Autumnal aspect.* In late September there are chilly days, and the first of the winter visitors among the birds appear. By the first week in October the few lingering hooded warblers and scarlet tanagers have gone, and other summer resident species are probably represented by late migrating individuals only. The first robins and thrushes are noted in the woods—the prophecy of many more to come. October sees great flocks of them—robins in two great waves, the flocks numbering hundreds—and thrushes—hermits first, then olive-backs, veerys, and gray cheeks. They feast upon the wild grapes, the fruits of tupelo, sassafras, pokeweed, and flowering dogwood. They also give the floor of the forest a thorough looking over for beetles, grubs and other insects, as they turn over the dead leaves and dig into the rich humus. Their stay lasts into November, covering the period of the great fall of leaves from the deciduous trees. Meanwhile the winter visitors are increasing in number, and if the red-breasted nuthatch is present, these numbers may reach considerable proportions. The characteristic winter bird companies are now formed and will keep together throughout the winter.

Color in the forest in autumn develops later than it does along the roadsides, and many trees retain their leaves long after the roadside trees are bare. Elm, tulip, and spicebush begin the process by yellowing early. October 10th sees the first splashes of real color inside the forest, though it will be ten days at least before the woods are all red and gold. Robins are noisy, sounding alarms, calling, and occasionally carolling a bit. Chipmunks add to the racket, chippering and clucking everywhere, and are very active about the grape vines. Both red and gray squirrels are vocal. Blue jays are calling, white-throated sparrows singing in the grape tangles, nuthatches signaling from nearby trees. The green leaves of wild ginger are still bright in places where this plant occupies the ground.

By mid-October, though the interior of the forest is still predominantly green, the tops of the trees show yellow, bronze, and red. The tupelos are quite red. By October 27th the leaves are about half off the trees, and now rains and high winds will begin stripping off all those that have loosened

their grip upon the twigs. In the absence of wind the leaves will fall lazily by ones and twos. Sugar maples and beeches are the last to surrender their leaves to the winds and often small beeches will retain their leaves, dead and brown, throughout the winter. These newly fallen leaves make a transitory carpet of red, yellow, and brown on the forest floor. With the falling of the leaves of the primary dominants beech nuts and maple seeds also are shed in large quantities, and storage activities on the part of chipmunks, red squirrels, and gray squirrels becomes a major activity. Numbers of gray squirrels may increase as individuals from outside the area come in attracted by the abundance of food. There is liable to be a full chorus of chipmunk clucking which may be taken up and carried throughout the entire range of woodland as far as the ear can discern it.

The first week in November sees the forest floor first yellow, then changing through bronze to brown. There are large open spaces in the forest roof, and the dark green of hemlocks begins to show in the background as one faces the areas where the beech-hemlock association has its stand. Voices of towhee, nuthatch and junco are characteristic of this period, and bob-whites may come into the deep woods attracted by the beech nut supply. The trees will be bare by the third week in November. This is still a period of great activity among birds and mammals, and there are days when they are very vocal, and when *Hyla crucifer* adds his voice to the chorus.

6. *Hibernal aspect.* There is no sharp demarcation between autumnal and hibernal aspects. Indian summer days may be extended through November, though snow usually comes before the month is well advanced. Tree trunks are now a feature of the aspect, the light gray of beech and the dark brown of sugar maple making a fine contrast. With the coming of the first real snow-blanket the woods present a record of moving animal life written upon its white surface. This is one of the characteristic aspects of winter. At times the tracks of gray squirrels will cover every part of the area. These animals, with red squirrels and chipmunks, will be noted abroad throughout the winter, and will write most of the story on the snow. Tracks of cottontail rabbit, red fox, white-footed mouse, and short-tailed shrew will be commonly seen. This is the time of hibernation for invertebrates and some vertebrates as well. In December, January, and February the species list of birds is restricted to the permanent resident and winter visitor groups, with a massing of numbers in December and a low point in late January.

A feature of the hibernal aspect is made up of the green leaves which a number of plants carry over winter. Prominent among these is the hepatica. Others are foam flower, bishop's cap, wild blue phlox, spring cress, and some violets, together with christmas fern, spinulose wood fern, marginal shield fern, and shining club moss. The sedge *Carex* shows green clumps

throughout the winter along the edges of the ravines. As the winter progresses the débris of stored foods appears where it is dug up and consumed by the squirrels, and one can form a fairly good opinion as to just what foods are mostly depended upon for winter needs.

Winter in the area under study is a period of high humidity, due to the fact that snow does not usually stay upon the ground for any great length of time, and temperatures are frequently above the freezing point. This means much melting of ice and snow and much standing water in pools. The atmosphere is often filled with mist and the snow saturated with water.

PLANTS AND ANIMALS

The fundamental difference between plants and animals is, of course, that plants manufacture their own foods out of elemental substances, while animals do not, but must in the last analysis depend upon the products of plants for their supplies of food. Seasonal behavior on the part of the animal population of a biotic community is thus closely correlated with seasonal changes in plant activities. Aspection, from the standpoint of the animal population is but a shifting of food supplies—a sort of clearing and resetting of the table. On the other hand, in their search for and gathering of food, and through other activities, animals in turn affect plants in various ways.

Seasonal responses of animals to the activities of plants are well illustrated in the present study. Such responses may be direct, as when the animal is directly dependent upon plant materials for food, or indirect, as when the animal is dependent upon other animals for its food. The following sequence of observed events in the area under study is illustrative of such relationships.

With the blossoming of the early wildflowers in April winged insects appear. These are attracted to the pollen and nectar offered by the flowers, and their activities assist in the cross-pollination of the plants. The phoebe (a flycatcher) now comes into the woods, feeding upon the flying insects as an acceptable food supply.

With the swelling of the buds on the forest trees in spring, gray squirrels climb aloft to sample this new offering of food, and such birds as the purple finch and the rose-breasted grosbeak make their appearance as consumers of this plant product.

With the expansion of the leaves on the trees, hatching insect eggs produce a multitude of caterpillers as consumers of new foliage. With the appearance of this new food supply for birds, come hosts of migrating warblers whose arrival is neatly timed to coincide with the opportunity to glean many of these minute larvae from the developing foliage. The summer resident birds, all highly insectivorous, now arrive from their southern winter-

ing quarters and replace the early transients as consumers of enormous numbers of insects.

With the storage of carbohydrates in roots, tubers, and other underground structures of herbaceous plants, chipmunks begin to nose the ground and to plow up many of these crisp foods. They also feed upon blossoms and developing seeds.

With the ripening of forest fruits, birds and rodents become very active about the bearing trees and vines and lesser growth as they feast upon these newly offered foods.

With the development of the great forest crop of gilled mushrooms, a new assembly of insects becomes active as a consumer of this plant product, and many rodents also seek it out as a new food.

With the falling of nuts and seeds from the trees, activity on the part of mice and squirrels becomes strenuous as they gather these staple foods for storage against future needs.

With the arrival of winter inactivity in the plant world the animal population exhibits a number of differing responses to this radical change in conditions. Some species migrate to other places, some go into hibernation, some live upon the stored food which they have gathered and laid away, some increase their resistance to lowered temperatures and go on hunting as before.

Basically the forest dominants must be considered as the determiners of the whole complex of life within the range of their influence. They, of course, depend upon soil and climate for their existence where they are, but being there, they not only *limit* and *circumscribe* the life activities of other organisms associated with them, but *vitalize* them as well. The limiting influence of the forest on other organisms is expressed through such things as occupation of the ground, cutting down of light, increasing relative humidity, reducing rate of evaporation, modifying temperature—matters which in the present study have been considered under the head of climate. Species which are not equipped to live in such an environment are excluded. The vitalizing influence of the forest is expressed through the production of stored energy of such quality and quantity, and in such form, as to be readily available to the animal population as food.

The beech-maple forest thus limits and supports an enormous insect population which not only consumes vast amounts of plant material, but which also has many complex interrelations within its own group and with other animals; a rodent population adapted to the use of beech nuts and sugar maple seeds; a shrew population that spreads its network of tunnels beneath the humus for the capture of insects and other prey; a woodpecker-nuthatch-flycatcher-thrush population adapted to the capture of insects in many different situations above ground; and a relatively small carnivore

group which subsists upon the smaller vertebrates. The mammals are predominantly seed and insect eaters, the birds predominantly insectivorous. Chains of animals are thus linked together by food, and all dependent in the long run on plants. Thus we have the concept of the food chain and the food cycle (Elton 1927).

In addition to an adequate food supply, the numbers of animals to be found within a forest community are greatly influenced by the facilities offered for successful reproduction and for protection from enemies. From the standpoint of birds and mammals this means cover, nesting sites, nesting materials, and satisfactory adjustment to the environment during the breeding season. It is because the forest under study is rich in these respects that such a large animal population as has been noted at times is possible.

From the standpoint of the effects of animal activities upon plant life the fact of outstanding significance is the very large consumption of plant materials by insects. Not only is the steady consumption of foliage by the larvae of many species involved, but no part of the plant structure is immune from attack. Buds, leaves, blossoms, bark, sapwood, heartwood, twigs, leaf petioles, root structures, seeds, juices—all have their specialized groups of insects adapted to feed upon them, or to utilize some of them for purposes of pupation or hibernation. The effects of such activities on plants are essentially destructive.

Over against this potentially grave destructive force, and mitigating its effects in large degree, is the ever-present fact that insects are hunted and consumed as food by practically the entire bird and mammal population, the entire spider population, and a considerable group within their own ranks. It is to this insect-consuming group of animals that the forest owes its continued existence, for it seems a fair assumption that if the activities of the birds and mammals and predaceous insects of the forest community were withdrawn or nullified in some way, the forest would soon be destroyed by the unchecked ravages of phytophagous insects.

It is true that many birds and mammals are also consumers of buds, leaves, shoots, bark, and roots of plants. While all of this has its limiting effect on plant life, it is inconsequential as compared with the effects of insect consumption of plants or of competition among plants themselves. The large consumption of seeds by birds and mammals is also inconsequential, except possibly in years of low seed production, as seeds are produced normally in enormous quantities and there is a very large surplus over and above the needs for reproduction. In fact, with the ever-present threat of serious injury to the forest dominants through the destructive activities of insects, the conversion of the surplus seed supply directly or indirectly into insect-consuming animals appears as a necessary protective

measure and a part of the mechanism whereby equilibrium in the community is maintained.

The animal population of the forest may thus be considered in relation to its effect upon plant life from two points of view—primarily as a severely limiting or potentially destructive force, as represented by the phytophagous insects, and secondarily as a protective and conserving force, as represented by the predaceous insects, spiders, birds, and mammals. In this connection it is interesting to consider how largely insects enter into the regular diet of animals usually classified as more or less strictly herbivorous or carnivorous.

The storage of nuts underground by squirrels has often been referred to as a kind of "planting" of seeds, beneficial to the forest, when such seeds are not later dug up and eaten but are left to sprout. This may be the case in areas where reforestation is in progress, but in the already established forest it is negligible as compared to the natural and normal seeding of the forest trees which is usually far in excess of the need.

An important contribution made by animals to the well-being of the plant community which should not be overlooked lies in the vast amount of stirring up of the soil that they accomplish. Shrews, mice, moles, and chipmunks are great tunnelers in soil and humus and dead wood. Many invertebrates, like the ants that work in dead wood, the insects that live under dead bark, earthworms, and many animals of minute size that are active in the humus (Jacot 1935), all contribute to this result. The plowing of the ground by red squirrels and gray squirrels as they prosecute their search for buried food is somewhat in the nature of continuous cultivation, and there is constantly added from their droppings, and from those of countless other animals, an enrichment of the soil that in the aggregate must bulk very large. Some of this stirring up of the soil is of benefit to the more deeply rooted plants in freeing them from competition with more insecurely rooted neighbors. Thus the chipmunk, nosing out the tubers of spring beauty or dwarf ginseng, makes better the conditions for growth for the seedling beech crowded in among the vigorous herbs.

Because of such interrelations plants and animals form a sociological unit, the biotic community, making a consideration of either without the other incomplete.

SUMMARY AND CONCLUSIONS

The subject of the study herein presented is a 65 acre tract of beech-maple-hemlock forest in the Cleveland, Ohio, Metropolitan Park System. Systematized work was carried on through regular weekly visits covering a period of four years. Records of temperature, precipitation, relative humidity, wind velocity, and evaporation rate were obtained.

2. Considering the vegetation of the area as a whole, it is evident that there exist here two rather distinct forest communities; a beech-maple association and a beech-hemlock-oak-chestnut mictium.

3. The beech-maple association represents the climatic climax of the region. It is mature, vigorous, stable, well established, and occupies 89 per cent of the area. It is characterized principally by the beech and the sugar maple as primary dominants, with red maple, tulip, white ash, and northern fox grape as secondary dominants. Shagbark hickory, cucumber, red oak, and white oak are listed as incidental dominants, and hop hornbeam and American hornbeam as subdominants. Other subdominant species include 12 of shrubs, 69 of herbaceous plants, 14 of ferns, 7 of climbing, twining, or trailing plants, 10 of mosses, and 6 classified as miscellaneous. Of saprophytic and parasitic plants 247 are listed. Seasonal aspects, including the responses of both plants and animals to seasonal changes, are described.

4. The beech-hemlock-oak-chestnut mictium represents a remnant of former forest communities now giving place to beech-maple. It is unstable, lacks vigor, is not well established, occupies 11 per cent of the area. It is characterized principally by the beech, the hemlock, and formerly the chestnut, as primary dominants, with red maple and red oak as secondary dominants. Shagbark hickory, cucumber, tupelo, sassafras, white oak, wild black cherry, pignut, black birch, and scarlet oak are listed as incidental dominants, and hop hornbeam and American hornbeam as subdominants. Other subdominant species include 7 of shrubs, 1 of climbing plants, 6 of herbs, and 5 of ferns.

5. One of the primary dominants of the mictium, the beech, represents the entering wedge of the climatic climax. Another, the hemlock, represents a more northern forest community left in its present position apparently as a remnant of the forest which followed the glacial ice in its northward retreat. In this community the presence of certain subdominants usually associated with hemlock is noted. The oak-chestnut remnants on the other hand represent a prominent forest community now to be found in the southern Appalachians.

6. As compared with the plants of the area the animal content presents a constant fluctuation in numbers, species, and activities. A study of the vertebrates and some invertebrates discloses the presence of 27 species of mammals, 83 of birds, 8 of reptiles, 11 of amphibians, and 20 of molluscs.

7. A study of the numbers and distribution of these animals indicates that all habitats and ecological niches in the area are well occupied when the population is at its peak, but that great changes in numbers occur both seasonally and annually. The most abundant mammals were found to be the short-tailed shrew and the white-footed mouse. Of birds 11 species were

classed as permanent residents, 8 as autumn and winter visitors, 16 as summer residents, 23 as transients, and 25 as occasional visitors. The number of nesting pairs per acre was found to average 2.3 (5.7 per hectare). Of the reptiles only one, the pilot blacksnake, was found to have important ecological relations.

8. The constituent animal species, exclusive of invertebrates, classified on the basis of abundance, activities, and influence in the community were assigned the following positions: permanent predominants 7, fluctuating predominants 3, seasonal predominants 15, permanent members 11, fluctuating members 2, seasonal members 47, incidental members 37.

9. The interrelations between plants and animals are considered, and the conclusion is reached that a consideration of either without the other is incomplete.

LITERATURE CITED

Adams, C. C. 1906. An ecological survey in northern Michigan. *Rpt. Mich. State Bd. Geol. Surv., for 1905.* pp. 9-12.

——— 1908. An ecological survey of Isle Royale, Lake Superior. *Rpt. Mich. Biol. Surv.* 468 pp.

American Ornithologists' Union Committee. 1931. Check list of North American birds, 4th ed. 526 pp. New York.

Anthony, H. E. 1928. Field book of North American mammals. 625 pp. New York.

Bird, R. D. 1930. Biotic communities of the aspen parkland of central Canada. *Ecology* **11**: 356-442.

Blake, I. H. 1926. A comparison of the animal communities of coniferous and deciduous forests. *Ill. Biol. Monog.* **10**: 1-148.

Board of Park Commissioners of the Cleveland Metropolitan Park District. 132-33. *Ann. Rpt.* 91 pp. Cleveland.

Boettger, C. R. 1934. Die Abwehr der Landschnecken gegen Käfer. Natur and Volk **64**: 380-384.

Boycott, A. E. 1934. The habits of the land Mollusca in Britain. *Jour. Ecology* **22**: 1-38.

Bray, W. L. 1915. The development of the vegetation of New York State. *N. Y. State Col. Forestry Tech. Pub.* **3**:186 pp.

Burns, G. P. 1923. Minimum light requirements referred to a definite standard. *Vt. Agr. Expt. Sta. Bul.* **235**: 32 pp.

Butts, W. K. 1931. A study of the chickadee and white-breasted nuthatch by means of marked individuals. *Bird-Banding* **2**: 59-76.

Cahn, A. R. and J. T. Kemp. 1929. The terrestrial molluscs of Turkey Run State Park, Indiana. *Ill. State. Acad. Sci. Trans.* **22**: 250-262.

Cain, S. A. 1932. Studies on virgin hardwood forest: 1. Density and frequency of the woody plants of Donaldson's Woods, Lawrence County, Indiana. *Ind. Acad. Sci.* **41**: 105-122.

Chapman, R. N. 1931. Animal ecology with special reference to insects. 464 pp. New York.

Clements, F. E. 1916. Plant succession. *Carnegie Inst. Wash. Pub.* **242.** pp. 184-237.

Clepper, H. E. 1931. The deer problem in the forests of Pennsylvania. *Penna. Dept. Forests and Waters, Bul.* **50.** pp. 43.

Coffey, G. N. and T. D. Rice. 1912. Reconnoissance soil survey of Ohio. *U. S. Dept. Agri. Bur. Soils.* Advance Sheets. pp. 69-76.

Cushing, H. P., F. Leverett, and F. R. Van Horn. 1931. Geology and mineral resources of the Cleveland District, Ohio. *U. S. Geol. Surv. Bul.* **818.** 138 pp.

Daubenmire, R. F. 1930. The relation of certain ecological factors to the inhibition of forest floor herbs under hemlock. *Butler Univ. Bot. Studies* **1**: 61-76.

Dearborn, N. 1932. Foods of some predatory fur-bearing animals in Michigan. *Univ. Mich. Bul.* **1**:52 pp.

Dice, L. R. 1920. The mammals of Warren's Woods, Berrien County, Michigan. *Mich. Univ. Mus. Zool. Occas. Papers* **86.** 20 pp.

Ditmars, R. L. 1920. The reptile book. 472 pp. New York.

Elton, C. 1927. Animal ecology. New York and London.

——— 1930. Animal ecology and evolution. Oxford.

Esten, M. M. 1932. A statistical study of a beech-maple association at Turkey Run State Park, Parke County, Indiana. *Butler Univ. Bot. Studies* **2**: 183-201.

Fisher, A. K. 1893. The hawks and owls of the United States in their relation to agriculture. *U. S. Dept. Agri. Div. Ornithol. and Mammal. Bul.* **3**: 210 pp.

Forbush, E. H. 1925-27-29. Birds of Massachusetts and other New England States. 3 vols. *Mass. Dept. Agri.* Boston.

Frothingham, E. H. 1915. The northern hardwood forest: its composition, growth, and management. *U. S. Dept. Agri. Bul.* **285**: 80 pp.

Gleason, H. A. 1924. The structure of the beech-maple association in northern Michigan. *Mich. Acad. Sci., Arts, and Letters, Papers.* **4**: 285-296.

Hamilton, W. J. 1933. Notes on the food of red foxes in New York and New England. *Jour. Mammal.* **16**: 16-21.

Harshberger, J. W. 1911. A phytogeographic survey of North America. 790 pp. Stechert, New York.

Howell, A. H. 1929. A revision of the American chipmunks. *U. S. Dept. Agri. North Amer. Fauna* **32.** 47 pp.

Illick, J. S. and Le Roy Frantz. 1928. The beech-birch-maple forest type in Pennsylvania. *Penn. Dept. Forests and Waters Bul.* **46.** 40 pp.

Jacot, A. P. 1935. Wild life of the forest carpet. *Sci. Mo.* **40**: 425-430.

Johnson, M. S. 1926. Activity and distribution of certain wild mice in relation to biotic communities. *Jour. Mammal.* **7**: 245-277.

Lengerken, H. von. 1934. Käfer auf der Schneckenjagd. *Natur und Volk* **64**: 375-379.

Leopold, A. 1935. Game management. 481 pp. New York.

Livingston, B. E. and F. Shreve. 1921. The distribution of vegetation in the United States as related to climatic conditions. *Carnegie Inst. Wash. Pub.* **284.** 590 pp.

Lutz, H. J. The vegetation of Heart's Content: a virgin forest in northwestern Pennsylvania. *Ecology* **11**: 1-29.

McDougall, W. B. 1927. Plant ecology. 326 pp. Philadelphia.

Miller, G. S. 1924. List of North American recent mammals. *U. S. Natl. Mus. Bul.* **128**: 673 pp.

Moore, B., H. M. Richards, H. A. Gleason, and A. B. Stout. 1924. Hemlock and its environment. *N. Y. Bot. Garden Bul.* **12**: 325-350.

Moseley, E. S. 1897. The climatic influence of Lake Erie on vegetation. *Amer. Nat.* **31**: 60-63.

Quick, B. E. 1923. A comparative study of the distribution of the climax association in Southern Michigan. *Mich. Acad. Sci., Arts, and Letters, Papers* **3**: 211-244.

Robinson, B. L. and M. L. Fernald. 1908. Gray's new manual of botany, 7th Ed. 926 pp. New York.

Sampson, H. C. 1927. The primary plant associations of Ohio. *Ohio Jour. Sci.* **27:** 301-309.

——— 1930. Succession in the swamp forest formation of northern Ohio. *Ohio Jour. Sci.* **30**:340-357.

Schiermann, G. 1930. Studien über Siedelungsdichte im Brutgebiet. *Jour. Ornithol.* **87:** 137-180.

Schooley, J. P. 1934. A summer breeding season in the eastern chipmunk, *Tamias striatus*. *Jour. Mammal.* **15:** 194-196.

Sears P. B. 1925-26. The natural vegetation of Ohio. *Ohio Jour. Sci.* **25:** 139-149, **26:** 128-146, 213-231.

Seton, E. T. 1909. Life histories of northern animals. 2 vols. New York.

——— 1929. Lives of game animals. 8 vols. New York.

Shantz, H. L. and R. Zon. 1924. The physical basis of agriculture: natural vegetation. Atlas of American agriculture. Pt. I, Sec. E. 29 pp. U. S. Dept. Agri., Bur. Agri. Economics, Wash., D. C.

Shelford, V. E. 1913. Animal communities in temperate America. 362 pp. Chicago.

Shelford, V. E. et al. 1926. Naturalists' guide to the Americas. 761 pp. Baltimore.

Shelford, V. E. and Sigurd Olson. 1935. Sere climax and influent animals with special reference to the transcontinental coniferous forest of North America. *Ecology* **16:** 375-402.

Shull, A. F. 1907. Habits of the short-tailed shrew. *Amer. Nat.* **41:** 495-522.

Smith, V. G. 1928. Animal communities in a deciduous forest succession. *Ecology* **9:** 479-500.

Transeau, E. N. 1905. Forest centers of eastern North America. *Amer. Nat.* **39:** 875-889.

Turner, C. L. 1926. The crayfishes of Ohio. *Ohio Biol. Surv. Bul.* **13:** 145-195.

U. S. Department of Agriculture, Weather Bureau. Monthly meteorological summary, Cleveland, Ohio. 1931 to 1935.

Von Schrenk H. and P. Spaulding. 1909. Diseases of deciduous forest trees. *U. S. Dept. Agri. Bur. Plant. Indus. Bul.* **149:** 73 pp.

Weaver, J. E. and F. E. Clements. 1929. Plant ecology. New York.

Weese, A. O. 1924. Animal ecology in an Illinois elm-maple forest. *Ill. Bot. Monog.* **9:** 1-93.

Zon, R. and H. S. Graves. 1911. Light in relation to tree growth. *U. S. Dept. Agri. Forest Serv. Bul.* **92.** 59 pp.

MOISTURE RELATIONS IN THE CHAPARRAL OF THE SANTA MONICA MOUNTAINS, CALIFORNIA

By

HARRY L. BAUER
Santa Monica, California

CONTENTS

MOISTURE RELATIONS IN THE CHAPARRAL OF THE SANTA MONICA MOUNTAINS, CALIFORNIA

INTRODUCTION

Chaparral is found extensively in California, especially in the foothills and mountain ranges of lower altitudes in the coastal portions of the central and southern parts of the state where it is a climatic climax type of vegetation. The most conspicuous characteristic of this community is the mass dominance of broad-sclerophyll shrubs.

As the chief vegetative cover of the watersheds of southern California, chaparral is of great economic importance in that it lowers the loss of water through surface run-off, increases the flow of clear water in streams, and decreases the probability of serious floods and erosion.

The investigation herein reported is concerned primarily with the moisture relations in a representative area of Californian coastal chaparral. In the first part of the paper there is a somewhat detailed account of the structure and other ecological features of this community. Following this, the environmental complex of the association is analyzed with particular reference to soil moisture and the evaporating power of the air as they are related to growth and other features of the vegetation. Consideration is also given to precipitation, atmospheric moisture, and temperature, especially soil temperature. An attempt is made to evaluate the several factors and to correlate them with the activities of the vegetation.

Instrumental work was begun with the week ending September 5, 1931. In all, fifteen research stations were utilized. These stations were visited and data collected weekly for an unbroken period of fixty-six consecutive weeks. After this four stations were selected for further observation. At these stations measurements were made at four-week intervals throughout the second year, terminating on August 28, 1933.

REVIEW OF THE LITERATURE

The first studies of chaparral were made from the standpoint of geography, taxonomy, and forestry. With few exceptions, noteworthy ecological investigations have been made only within the last decade. Of the accounts of the early European botanists who described the vegetation of western North America, that of Schimper (1903) was the first to be at all satisfactory. McKenney (1901) described in detail the several chaparral "formations" in the Santa Ana Mountains, California.

Leiberg (1899, 1900) described the chaparral of certain forest reserves. A number of minor articles by foresters and taxonomists appeared previous to 1920.

The first papers by Californian botanists were of a phytogeographical nature. Hall (1902) studied the chaparral zones of Mt. San Jacinto, and Parish (1903) and Abrams (1910) published descriptions of the scrub communities of the entire southern portion of California. Clements (1920) also described the communities of this area.

The first monographic ecological study was by Cooper (1922). In this, the Californian chaparral is considered from a number of different angles and there is included an account of intensive instrumental work on a representative area near Palo Alto. Shreve (1927) published the results of some instrumentation in the vegetation, chiefly chaparral, of the Santa Lucia Mountains, and Howell (1929) described the chaparral of Santa Ana Canyon. Papers by Whitfield (1932) were on transpiration and osmotic pressure in the chaparral near Santa Barbara, California, and one by Copeland (1932) was on transpiration and temperature in the chaparral of the northern Sierra Nevada. Shapiro and de Forest (1932) reported the results of transpiration studies in the chaparral of the eastern Santa Monica Mountains.

THE AREA

LOCATION AND TOPOGRAPHY

The Santa Monica Mountains, one of the outer coastal ranges in southern California, extend westward of the city of Los Angeles for about fifty miles. The main axis of the range is located at approximately 34° 5′ north latitude and its center is near 118° 40′ west longitude. The map (Fig. 1) shows the location and the relation of these mountains to some of the geographical and topographical features of this section of the state. It may be noticed that, unlike most Californian ranges, this one trends in an almost straight east-west direction. The Pacific Ocean lies along a considerable portion of the southerly base of the range and the San Fernando Valley along the northerly.

The topography of the area is rough. The highest peaks, which reach an altitude of about 3,000 feet, are located within three or four miles of the ocean. After the storms of the rainy season, the streams carry a large amount of water, but for the greater part of the year most of them are dry and the others carry such a small amount of water that those on the seaward side cannot keep their channels through the beach sand clear as far as the ocean, consequently forming lagoons bordered with a rank growth of vegetation that is in striking contrast to the chaparral on the nearby dry slopes.

The chief geological formations, the Topanga and Modello, are of the middle and upper Miocene origin respectively (Hoots, 1930, p. 88). The last anticlinal uparching of these mountains occurred in the late Pleistocene.

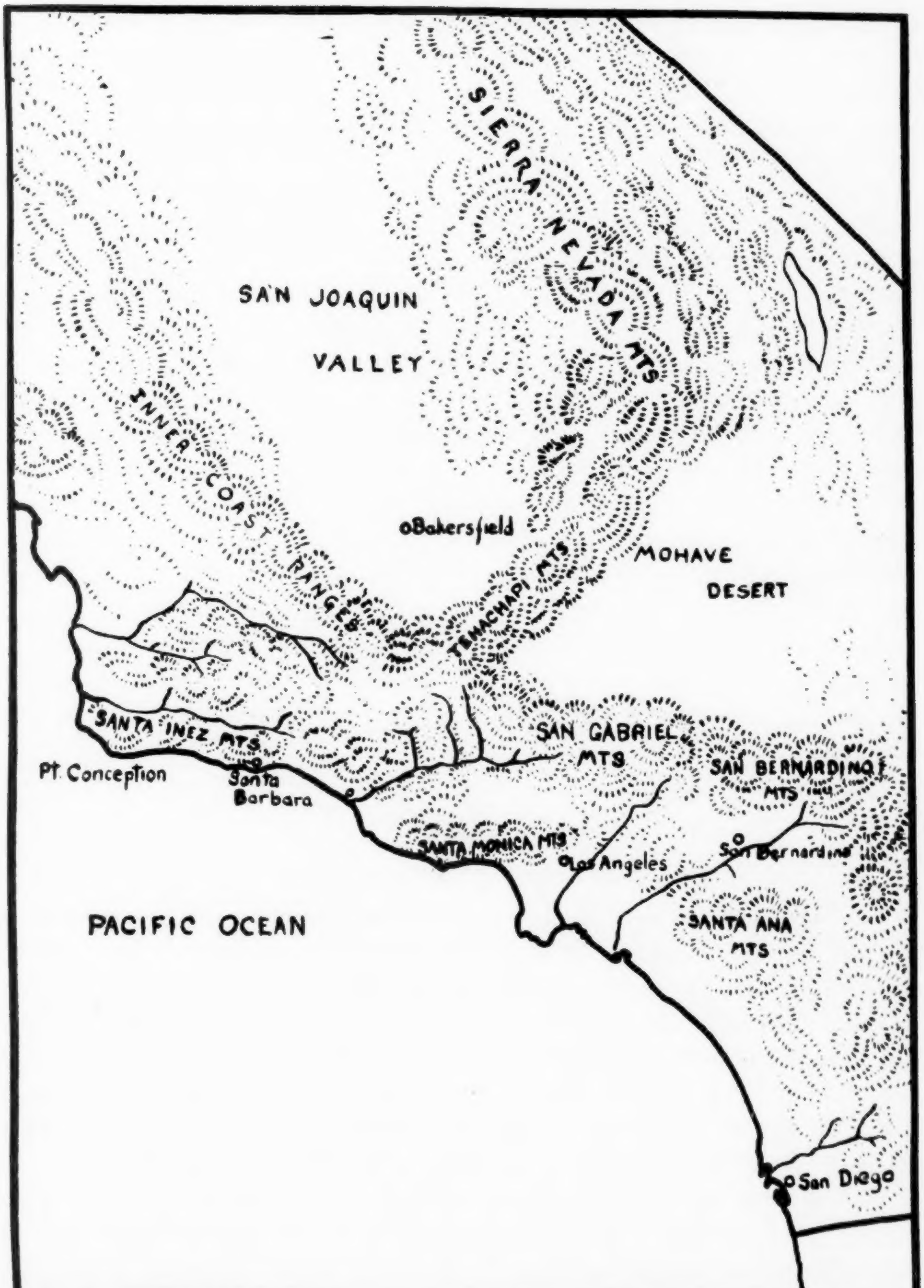

FIG. 1. Southern California showing the location of the Santa Monica Mountains, and their relation to other features.

The soils of most of the area are classified (Nelson, 1920) as "rough, broken, and stony land"; outcrops of rock are common. The layer of fine soil that has accumulated at some places within the mountain complex is

seldom more than a few feet in thickness. The alluvium at the bases of the mountains is much thicker but has no direct bearing on the chaparral of this study. Since the slopes are steep and the drainage generally good, accumulations of alkali do not occur in the soils of the area.

THE CLIMATE

The climate of the Santa Monica Mountains and of southern California in general is one of mild wet winters and hot dry summers, frequently designated as "Mediterranean climate." This climate, as it is found in California, has been carefully described by Russell (1926). The climatological records of the Los Angeles station of the United States Weather Bureau, which cover over half a century, are fairly applicable to the Santa Monica Mountains as to principal variations, although not necessarily as to exact amounts or intensities. These records show January to be the coldest month, having an average mean temperature of 55.1° F. August is the warmest month, having an average of 71.3° F.

The average annual precipitation at Los Angeles is about 15 inches per year, but in the nearby mountainous areas it is considerably greater, ranging up to 30 inches per year. More than 90 per cent of it comes during the six months, November to April. The average summer is practically rainless, having less than 2 per cent of the annual precipitation in the four months, June to September. Schimper (1903, pp. 465-469) has shown that each of the five widely separated chaparral areas of the world is correlated with a climate similar to that of the area here considered.

SITES FOR INSTRUMENTATION

The instrumental area was near the geographical center of the Santa Monica Mountains and is believed to represent well the chaparral of the entire range and also to be fairly characteristic of the coastal chaparral in general. According to Cooper's map of species density (1922, plate 1) this area lies just outside the region of greatest density, a region in which the vegetation is characterized by having from 21 to 25 chaparral species. The particular section chosen for instrumental work lies mainly along the ridges that lead toward Saddle Peak, and partly within Topanga Canyon.

The central part of the Santa Monica Mountains is traversed by a number of roads and a more or less elaborate network of firebreaks and trails constructed chiefly as a means of fire protection. The area is thinly populated, places of habitation being confined to a few summer resort subdivisions in the deeper canyons and a few widely scattered ranches. It is believed that the vegetation here has been very little disturbed by human activity.

The stations were established so as to represent varying conditions of vegetation, elevation, slope exposure, proximity to the ocean, and other

features. Stations 1 and 14 were near the ocean beach and not far above sea-level. Station 2 was about two miles inland and near the bottom of Topanga Canyon. Station 15 was near the base of the inland slope of the mountains and quite removed from the direct influence of the ocean. The remaining eleven stations were all located along a ridge of about 2,000 feet elevation and about three miles from the ocean. Of these, numbers 3 and 9 were near each other and on an area where the above-ground parts of the plants had been completely destroyed by fire one year previous to the beginning of the investigation. Station 4 was only about 50 feet from Station 3 but was located in characteristic chaparral that had not been burned in recent years. Stations 6 and 7 were established as characteristic easterly and westerly exposures, respectively, but were abandoned after four months because they were too greatly influenced by the conditions of the nearby general northerly exposure on which Station 5 was located. Stations 7, 11, 12, and 13 were all very similar except as to the direction in which the slopes faced, the four stations representing the four cardinal exposures. A summary of information on the stations is furnished in Table 1.

THE VEGETATION

COMMUNITIES ASSOCIATED WITH CHAPARRAL

The term chaparral has been used in a number of different ways. Some writers have applied it to any type of shrubby vegetation, even the desert scrub of the arid southwest. Clements (1920) uses the term in a broad sense and divides the community into two associations, (1) Petran chaparral, deciduous thickets found extensively in the Rocky Mountains, and (2) Coastal chaparral, the broad-sclerophyll vegetation of southern California. Jepson (1925) describes two types of chaparral in California, namely (1) soft chaparral, composed chiefly of deciduous species in the northern part of the state, and (2) hard chaparral, the same as the "coastal chaparral" of Clements. Cooper (1922) would restrict the use of the word to communities dominated by broad-sclerophyll shrubs, and recognizes two such associations in California, namely (1) climax chaparral, found especially in the southern part of the state, and (2) conifer forest chaparral, a successional form found associated with conifer forests in the northern part of the state. When the term chaparral is used alone in this paper, it refers to the coastal chaparral of Clements, the hard chaparral of Jepson, and the climax chaparral of Cooper, this being the ubiquitous plant community in the area considered.

In addition to the widespread chaparral, a few minor communities are present in restricted extent, namely (1) broad-sclerophyll woodland dominated by *Quercus agrifolia*,[1] (2) coastal sagebrush composed chiefly of

[1] All plant names are according to Jepson (1925).

TABLE 1. Summary of station data.

Station	Elevation ft.	Slope		Vegetation	Comments
		Degrees	Exposure		
1...	85	35	S	Coastal sagebrush.	"Sea-level" station. Near beach. Unprotected from ocean.
2...	400	35	S 5°E	Ceanothus type chaparral.	"Canyon" station. Topographically protected on three sides.
3...	2150	10	S 25°E	Recovering from recent burning.	"Burned chaparral" station. Plants sprouting from roots. Much bare ground.
4...	2150	10	S 35°E	Adenostoma type chaparral.	Characteristic unburned chaparral.
5...	2200	20	N	Quercus-Adenostoma type chaparral.	Representative northerly slope.
6...	2200	23	N 70°E	Adenostoma type chaparral.	Similar to 5; better protected.
7...	2200	22	N 70°W	Mixed chaparral species	Similar to 5; nearer ravine.
8...	2350	21	N 15°E	Quercus-Ceanothus type chaparral.	Tall chaparral of northerly slope.
9...	2100	17	N 35°E	Same as 3.	Same as 3.
10...	2200	10	N 90°W	Adenostoma type chaparral.	Representative westerly slope.
11...	2300	17	N 90°E	Adenostoma-Ceanothus chaparral.	Representative easterly slope.
12...	2375	25	N 90°W	Adenostoma type chaparral.	Representative westerly slope.
13...	2350	26	S	Adenostoma type chaparral.	Representative southerly slope.
14...	160	23	S	Ceanothus type chaparral.	Near 1 and a check upon it. Slightly better protected.
15...	1060	12	N 35°E	Mixed chaparral species.	At edge of San Fernando Valley. No direct ocean influence.

Salvia mellifera, Eriogonum fasciculatum, and *Artemisia californica,* (3) riparian or streamside association in which *Alnus rhombifolia* and *Platanus racemosa* are the most important species, and (4) a few small islands of grassland, doubtless the result of fire or other disturbances.

The ecotone between chaparral and the broad-sclerophyll woodland is not wide, the characteristic species mingling to only a very slight extent. However, between the chaparral and the coastal sagebrush, which usually occurs as a narrow zone at the lower edge of the chaparral where conditions are slightly more xeric, the boundary is very poorly marked, the chaparral appearing to be invading the sagebrush. This mingling is doubtless evidence of seral relation between the two communities.

ECOLOGICAL STRUCTURE OF CHAPARRAL

The most conspicuous feature of chaparral is the abundance of shrubs with broad evergreen leaves. In this growth trees are almost excluded and herbaceous plants are not abundant except along roads or other places where disturbances have occurred.

Under ordinary conditions the shrubs in this chaparral attain a height of about 2 m. Where exposed to the direct ocean winds they may be less than 1 m. and on the more favored northerly slopes they may be over 4 m. in height. Nevertheless the general appearance and uniformity of the chaparral mantle changes but little from canyon slope to hilltop. Something of the appearance of chaparral is shown in the photographs (Figs. 2 and 3).

Extensive studies of successions in chaparral have not been made. Some botanists question the climax character of the association, believing that, if it were not for the constantly recurring fires, the chaparral would eventually be replaced by a tree community. Cooper (1922, p. 82) is convinced that chaparral is a true climatic climax. His conclusion is based on the widespread dominance of this community, its evident stability, the fact that it occurs on sites of diverse soil and topography, and the obvious adjustment of broad-sclerophyll vegetation to climate. No areas can be found where chaparral similar to that of the Santa Monica Mountains is actually being replaced by other communities.

Secondary successions are frequently instituted by fires which denude the ground of vegetation, leaving no evidence of life above the surface (Fig. 9). During the first season after the fire, there usually appears a rank growth of herbs and also rapidly growing sprouts from the root crowns of the burned chaparral plants. The shrubs on the burned area investigated appeared to be about half regrown by the end of the third season after the fire. In a number of other places chaparral that had been burned about ten years previously was found to have resumed a normal appearance.

Transect studies showed that *Ceanothus macrocarpus* and *Salvia mellifera* were more abundant in young than in old chaparral, thus indicating that these species are more important in seral stages than in the climax. This probability is also indicated by the presence of numerous dead specimens in the older, but not younger, areas of chaparral. Shreve (1927, p. 38) notes that stands of certain species of *Ceanothus* serve as a nursery for seedlings of other species, and Cooper (1922, p. 87) states that chaparral with a large proportion of *Ceanothus* is likely to be a stage in secondary succession.

A successional stage five years after the chaparral was cut in the process of road construction is shown in the photograph (Fig. 5). The lighter colored vegetation next to the road is an almost pure stand of *Salvia mellifera*. In the adjacent uncut chaparral, this species did not appear except as small weak specimens. From this it appears that the black sage requires much light and cannot thrive after the chaparral shrubs exceed it in height. Its presence in marked quantity in the chaparral probably indicates fire or other disturbance not many years previously.

FIG. 2. Characteristic chaparral along the road leading to Saddle Peak. Elevation about 2,000 feet. Four stations, one on each cardinal exposure, were located near the top of the hill.

FIG. 3. Chaparral covered slopes of Topanga Canyon. Elevation about 400 feet. The mantle of vegetation has the same uniform appearance generally throughout the range.

FIG. 4. *Ceanothus spinosus* (mountain lilac) in full bloom in March. This shows something of the aspect of chaparral in late winter and early spring.

FIG. 5. Secondary succession after cutting vegetation in clearing road right-of-way. An almost pure stand of *Salvia mellifera* has grown up; climax chaparral above this.

SEASONAL ASPECTS

For a large part of the year chaparral shows little or no change in its appearance. After growth conditions become favorable in the early spring, however, there is a comparatively short period during which stems elongate, new leaves appear, and flowers and fruits are produced.

During the seasons considered in this investigation the flowering period of most species lasted for only a few weeks, but this period was not the same for all species. The result was that flowers were in evidence from January to July. The rather steady succession of flowers on chaparral species is shown in Figure 8. Blossoms appeared on the manzanitas in January before new leaves were produced. The time of greatest flowering activity, as judged by the number of species in bloom, was March and April. By far the most impressive display, however, occurred in February and March when the showy flower clusters on the widely distributed *Ceanothus macrocarpus* and *C. spinosus* seemed to transform the chaparral into a great garden (Fig. 4). Most of the broad-sclerophyll species characteristic of the climax chaparral were found to be in anthesis earlier, and to have shorter flowering periods than the suffrutescent and less sclerophyllous plants associated with the related communities.

FIRES

Fires have always been of frequent occurrence in chaparral. It is known that the aborigines, long before the time of white settlement, often fired the brush (Jepson, 1910, p. 11). Early settlers burned it periodically in the belief that it would improve grazing. In spite of elaborate present-day precautions to prevent them, the number of fires occurring annually in chaparral is surprisingly large. Records from the Los Angeles County Forestry Department show that for the period 1926 to 1934 an average of about 35 fires per year occurred in the Malibu Division of the Santa Monica Mountains, an area of about 200 square miles. Most of these were of insignificant size but one or two per year exceeded an area of one hundred acres.

As a means of determining the age of chaparral, or at least the time elapsed since the last fire, a large number of stems were cut and the annual rings counted. In much of the chaparral of the Santa Monica Mountains, no specimens over 12 years of age could be found. The oldest occurred in the vicinity of Station 8, where it was 26 years old. It is probable that no large percentage of chaparral is older. Lowdermilk (1933), in commenting on an area of chaparral on the east fork of San Dimas Canyon in the San Gabriel Mountains, states that it had not been burned for 50 years and that it had probably escaped fire as long as any chaparral in California.

FIG. 6. Specimen of *Photinia arbutifolia*. During the winter of 1931-32 many plants were undermined by heavy rains and fell into the roads, exposing much of their root systems.

FIG. 7. Station 8; north slope. Elevation 2,350 feet. The ground surface is covered with a comparatively heavy layer of litter and humus. Note the peculiar pitted appearance of the Ceanothus stems.

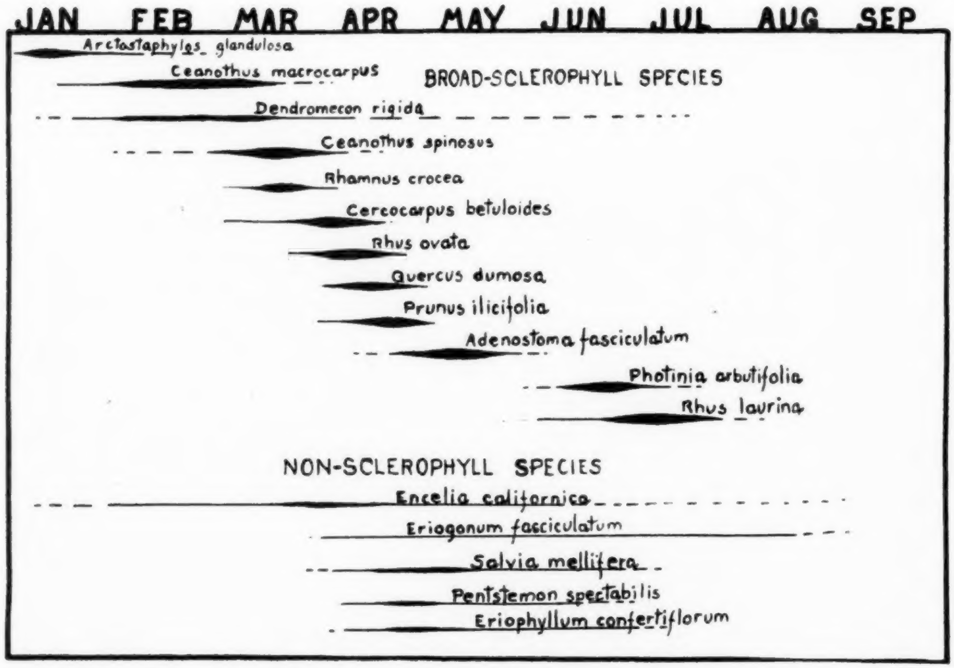

FIG. 8. Flowering periods of characteristic chaparral species in 1932.

All investigators agree that fire has contributed much to the present appearance of chaparral. It is believed to have affected the stature, form, and xeric characteristics of the plants. A number of species respond to repeated fires by developing, just below the surface of the ground, large, tuberous platforms, or irregularly shaped masses of woody tissue from which numerous stems may arise. Fires explain the evident lack of uniformity in the composition of chaparral. Two or more contiguous quadrats may show a strikingly different floristic make-up. A fire often does not sweep the area clean, but burns irregularly, leaving islands in the midst of the burned area, as shown in the photograph (Fig. 9). The new growth may be somewhat different from that of the unburned island and, thus, make for a lack of uniformity in the vegetation after recovery from the fire is complete.

TRANSECTS

As a means of getting accurate data on the structure of the vegetation, the line transect was found much more suitable than the chart quadrat. This was because of the great difficulty of plotting accurately the plants in a dense thicket. In running the transects a steel tape was used and a transect unit of 15 m. selected. Only the woody plants were considered. The actual distance that each plant spread over the line was recorded, thus giving a better basis for ascertaining the relative abundance of species

FIG. 9. Burned area near the site of Stations 3 and 9. Note the islands of unburned vegetation. Photographed a few weeks after the fire of August, 1930.

FIG. 10. Station 8; southerly exposure. Elevation 2,350 feet. Note the wooden standard used to support atmometers at different levels. Plants were held back when the picture was taken.

than would be the case if the plants were only counted and their size disregarded.

A tabulation of the results of 1,065 m. of line transects is furnished in Table 2. This includes various elevations, exposures, and localities but excludes measurements made on recently burned areas or other areas that for some reason were not representative of the true coastal type of chaparral.

TABLE 2. Summary of line transect data for chaparral.

Species	Per cent of total vegetation touching transect line	Per cent of transect distance covered	Number of times appearing	Average Distance (m.) spread over transect line by individual plants
SCLEROPHYLLOUS SPECIES:				
Adenostoma fasciculatum	38.6	57.0	515	1.17
Ceanothus macrocarpus	16.5	24.5	208	1.2
Ceanothus spinosus	0.38	....	8	0.76
Quercus dumosa	5.3	7.9	80	1.05
Rhus laurina	2.7	4.0	39	1.09
Rhus ovata	1.7	....	25	1.07
Photinia arbutifolia	0.77	....	14	.85
Prunus ilicifolia	2.2	....	23	1.48
Cercocarpus betuloides	0.93	....	17	.86
Arctostaphylos glandulosa	2.97	....	57	.82
Arctostaphylos glauca	1.97	....	17	1.82
Ceanothus oliganthus	1.34	....	36	0.56
Total	76.23	....	....	1.03 (Average)
NON-SCLEROPHYLLOUS SPECIES:				
Salvia mellifera	9.46	14.0	162	0.92
Salvia leucophylla	1.14	....	24	0.75
Eriogonum fasciculatum	2.99	4.4	88	0.53
Erigonum cinereum	.52	....	9	0.92
Encelia californica	.77	....	14	0.84
Lotus scoparius	.83	....	20	0.63
Isocoma veneta	.67	....	26	0.41
Artemisia californica	.45	....	12	0.60
Total	16.83	....	....	0.70 (Average)

Adenostoma fasciculatum was the outstanding species of this area, constituting 38.6 per cent of all the vegetation touching the transect line and covering 57 per cent of the distance measured. The species of second importance was *Ceanothus macrocarpus* which made up 16.5 per cent of the vegetation and covered about one-fourth of the line run, being, thus considerably less than half as extensive as Adenostoma. The species ranking third in abundance, *Salvia mellifera*, constituted 10 per cent of the vegetation but the figure gives the species more prominence than it deserves in undisturbed, mature, climax chaparral, because in such a community, the black

sage exists largely as impoverished specimens underneath the more characteristic chaparral shrubs where it is obviously not in control of the ground but yields evidence of a former successional stage in which it played a more important rôle.

In the summary of the transect data, Table 2, 20 species are listed. This includes all the species of any importance in this area, although a number of others were represented in insignificant amounts. Of the 20 species, 12 are classified as sclerophylls, and the others as non-sclerophylls. The distinction is based on the relative hardness and rigidity of the leaves although there are no definite standards for this character. Some of the species in the latter group, especially *Salvia mellifera* and *Eriogonum fasciculatum,* are somewhat sclerophyllous but they lack the degree of rigidity characteristic of the plants designated as sclerophylls.

The first column of the table gives the percentage of vegetation as based on the sum of all the distances of all the plants measured on the transect line. The second column gives the percentage of the transect distance, that is to say, the length of the transect line, for each species. In the third column are given the number of times the species appeared on the line, and in the fourth column the average distance that the individual plants of each species covered the transect line. This is not, be it noted, the diameter of the plant crown, because the line does not cross the center of the crown in most cases. The procedure does show, though, the relative sizes of the plant bodies. Thus the crowns of the non-sclerophylls are about one-third smaller than those of the sclerophylls.

The line transect method described above was used to determine the differences in composition and structure on the cardinal exposures. The four stations (8, 11, 12, and 13) utilized for this were all located near the top of a hill shown in the photograph (Fig. 2) and were all topographically very similar except as to the matter of the direction toward which the slope faced.

A summary of the results is given in Table 3, in which only the more important species are considered. *Adenostoma fasciculatum* was found to be the most abundant on all exposures. On the southerly-facing slopes it constituted 58.8 per cent of the vegetation touching the transects and covered over 70 per cent of the transect line. *Adenostoma* was over four times as abundant on this exposure as the species of second importance, *Ceanothus macrocarpus.* The more xeric conditions of the southerly slopes do not favor the broad-leaved species but seem to have little effect on *Adenostoma.* The easterly and westerly slopes were intermediate with reference to the abundance of *Adenostoma,* the westerly having a little more, thus indicating, perhaps, more xeric conditions.

.*Quercus dumosa* appears to be sensitive to slight differences in environ-

TABLE 3. Percentage of species touching line transects run on different exposures.

Species	North	East	South	West
Adenostoma fasciculatum	24.2	40.0	58.8	47.5
Ceanothus macrocarpus	23.2	25.3	14.5	9.2
Quercus dumosa	14.8	3.7	0.5	0.0
Rhus laurina	0.3	0.0	4.6	4.3
Rhus ovata	3.1	0.0	0.0	4.8
Arctostaphylos glandulosa	9.0	0.0	0.0	0.0
Arctostaphylos glauca	4.6	4.0	2.6	0.0
Salvia mellifera	1.1	24.4	8.5	27.4
Eriogonum fasciculatum	0.8	2.1	6.8	3.0
Overlap	58.0	34.8	30.9	37.4
All sclerophylls	95.5	73.5	83.0	68.0
Bare ground	7.2	5.5	12.1	4.3

ment. It was here almost wholly confined to the northerly exposures, where it constituted 14.8 per cent of the vegetation. There was a little on the easterly and practically none on the westerly or southerly exposures. *Arctostaphylos* was more common on the northerly than on the southerly slopes. *Salvia mellifera* was almost excluded from the northerly but was rather common on the other exposures.

Since the branches of neighboring shrubs are usually interlaced, a given area of ground is often covered by more than one plant and species. The extent of this double or triple covering is indicated in Table 3 by the term "overlap." This was 30.9 on the southerly exposures, and 58 per cent, or nearly two times as much on the northerly ones, with the easterly and westerly exposures intermediate.

In spite of the marked overlap some bare ground is usually encountered in traversing chaparral areas. This has been averaged for the different exposures, the southerly ones exhibiting the largest amount, namely, 12.1 per cent.

The dominance of broad-sclerophyll vegetation, including the one narrow-sclerophyll, *Adenostoma*, is very obvious. This type of vegetation ranged from 68 per cent on westerly slopes to 95 per cent on the northerly ones.

THE ENVIRONMENT

PRECIPITATION

The rainfall data obtained in this investigation are supplemented by records of other agencies, namely, the Los Angeles station of the United States Weather Bureau, the Los Angeles County Forestry Department, and the Los Angeles County Flood Control District. The diagrams in Figure 11 are based on the records of the U. S. Weather Bureau at Los Angeles. The top diagram shows the average monthly rainfall for this station for a period of over half a century. The middle diagram is for the single season of

1931-1932, the period during which weekly visits were made to all the stations of the present investigation. At the bottom is shown the season 1932-1933, the second year of this investigation.

It may be noted that the season 1931-1932 approached the theoretical average year about as closely as any one year is likely to do, in that the total was only slightly above normal and in that the important rains began in November and continued for several months. The most noticeable difference between this particular year and the average is the sudden ending of substantial rainfall with the end of February. The precipitation for the second year of the investigation was markedly different from the average in both amount and distribution, although it is not at all unusual for well over half of the annual rainfall to occur during a single month, as was the case in 1932-1933. Thus the general precipitation conditions during the course of the field work herein reported were not unusual.

The total rainfall for the year 1931-1932 for a number of locations in and near the area investigated is presented in Table 4. Some of these stations were near the ocean at the southern base of the range; some at the edge of the San Fernando Valley at the northern base; and others at various elevations within the mountains proper. Contrary to what might be expected, the rainfall near the ocean was considerably less than farther inland. For this one season it was more than 20 per cent greater at the northerly base of the mountains than it was at the southerly base, near the

TABLE 4. Total annual precipitation for the season of 1931-1932 for several stations in or near the central portion of the Santa Monica Mountains.

Station	Elevation	Precipitation
Near ocean at the south base of the mountains:	*Feet*	*Inches*
Mouth of Topanga Canyon[1]	85	19.55
Bel Air Bay Club	90	13.52
Average	....	16.53
Within the mountainous area:		
Malibu Headquarters	747	28.23
Saddle Peak Road[1]	2200	30.17
Crag's Country Club	600	25.23
West Saddle Peak	970	25.61
Topanga Summit	1560	21.08
Average	....	26.06
Near San Fernando Valley at north base of the mountains:		
Girard	892	18.09
Calabasas	950	19.68
Adohr Dairy	815	19.58
Average	....	19.11

[1]Data for these stations taken from original records of this investigation. Data for all other stations taken from records of the Los Angeles County Flood Control District.

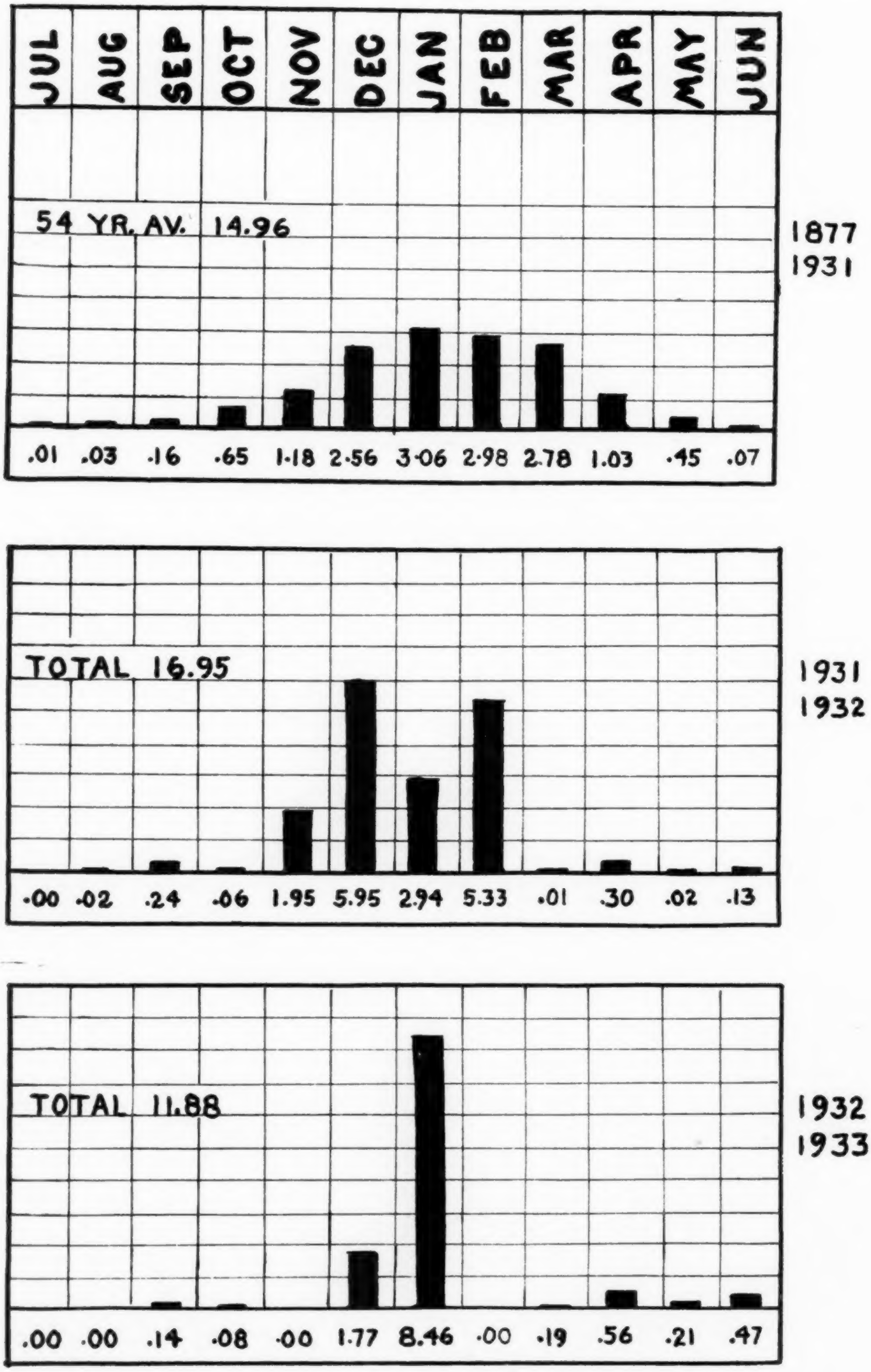

FIG. 11. Monthly distribution of rainfall at Los Angeles, California.

ocean. The variation among the mountain locations was considerable. For instance, Crag's Country Club, with an altitude of only 600 feet, had practically the same amount as the stations located at altitudes three or four times higher, but Topanga summit, with an elevation of 1,560 feet, located in the same canyon as Malibu Headquarters with an elevation of 747 feet, had considerably less rainfall than the latter station. It would appear from these facts that altitude is of less importance than distance from the ocean in influencing the amount of rain. The smaller amount near the ocean doubtless explains in part the more xeric character of the coastal sagebrush located there.

The direction in which a slope faces has considerable influence on the amount of rainfall received. In the Santa Monica Mountains, for the season of 1931-1932, the combined northerly and easterly slopes had about 20 per cent more than the southerly and westerly ones. A summary of results of the heavy rains is given in Table 5. The measurements were made by 3-inch U. S. Weather Bureau type rain gauges placed at Stations 8, 11, 12, and 13, all of which were located at about the same level on the hill shown in Figure 2. The differences in rainfall on the several exposures doubtless contribute considerably to the differences in vegetation, as previously described.

TABLE 5. Comparison of rainfall on different exposures during certain periods of heavy rainfall.

Period	Northerly	Easterly	Southerly	Westerly
	Inches	Inches	Inches	Inches
January 30 – February 6, 1932	5.22	5.46	4.41	4.00
February 6 – February 13, 1932	5.60	6.05	5.05	5.18
February 13 – February 20, 1932	1.32	1.47	1.39	1.34
January 15 – February 13, 1933	14.20	14.85	11.64	11.96
Total	26.34	27.81	22.49	22.48

Some rainfall interception data were yielded by gauges placed under the foliage of certain species, all of which were located near station V. The results are summarized in Table 6 for three species, namely, *Adenostoma fasciculatum*, *Ceanothus macrocarpus*, and *Arctostaphylos glandulosa*, and show that 70, 66, and 57 per cent, respectively, of the rain passed through the leafy crowns of the plants. The average of intercepted rainfall for all three species was about 35 per cent. Some of this reached the soil by way of stems and trunks and the balance was returned to the air by direct evaporation. For the light rains at the beginning and end of the wet season, such interception is an important source of loss. It is interesting to note that the species with the smaller leaves intercepted less rain than those with larger leaves. This may explain in part the greater success of the narrow-

TABLE 6. Rainfall in the open and under the foliage of nearby chaparral shrubs, 1931-1932.

Date	In the open	Under Adenostoma	Under Ceanothus	Under Arctostaphylos
	Inches	Inches	Inches	Inches
September 26	.05	.03	.03	.01
October 3	.13	.04	.07	.05
October 24	.23	.10	.13	.12
November 21	1.25	.86	.85	.75
November 28	2.97	2.83	2.07	1.53
December 12	1.87	1.54	1.46	1.30
December 19	1.15	1.13	.90	.94
December 26	4.00	2.15	2.56	2.22
January 2	4.90	2.88	2.98	2.64
Total	16.55	11.56	11.05	9.56
Per cent passing through plant	....	70.00	66.00	57.00

leaved *Adenostoma*, especially on the drier southerly exposures where it is more abundant than on other slopes.

SOIL MOISTURE

Samples of the soil for moisture determinations were cut from the walls of freshly dug trenches at all stations, on the occasion of each weekly visit. In nearly all cases samples were taken at two levels, namely, 10 cm. (surface) and 30 cm. (sub-surface), and at Station 8, where the soil was deeper, they were also taken at depths of 60 and 100 cm. The samples were dried in an electric oven at a temperature of 110° C. for a period of 48 hours. Weighings were in centigrams and the percentages of moisture calculated on the basis of oven-dry soil.

In order to get accurate information as to the capacity of these soils to retain moisture, and the amount of water readily available to the vegetation, determinations were made of both the moisture equivalents and the permanent wilting percentages.[1] The moisture equivalents were determined with a centrifuge according to the method of Briggs and Shantz (1912) and the results were used for the indirect calculation of the wilting coefficient. For the direct calculation of the permanent wilting percentages a slight modification of the Veihmeyer method was used. In this, dwarf sunflower seedlings were grown in glass tumblers having tin lids with small holes for the stems of the plants, and the moisture content was determined when the plants attained the permanent wilting point. The direct determinations were used as the basis of the wilting coefficient graphs in Figures 12 and 17, as the direct method has been found to be more accurate (Veihmeyer

[1] All of the determinations of moisture equivalents and some of those of wilting coefficients were made for the writer in the soil laboratories of the Graduate School of Tropical Agriculture and Citrus Experiment Station at Riverside, California, through the kindness of Professor S. H. Beckett.

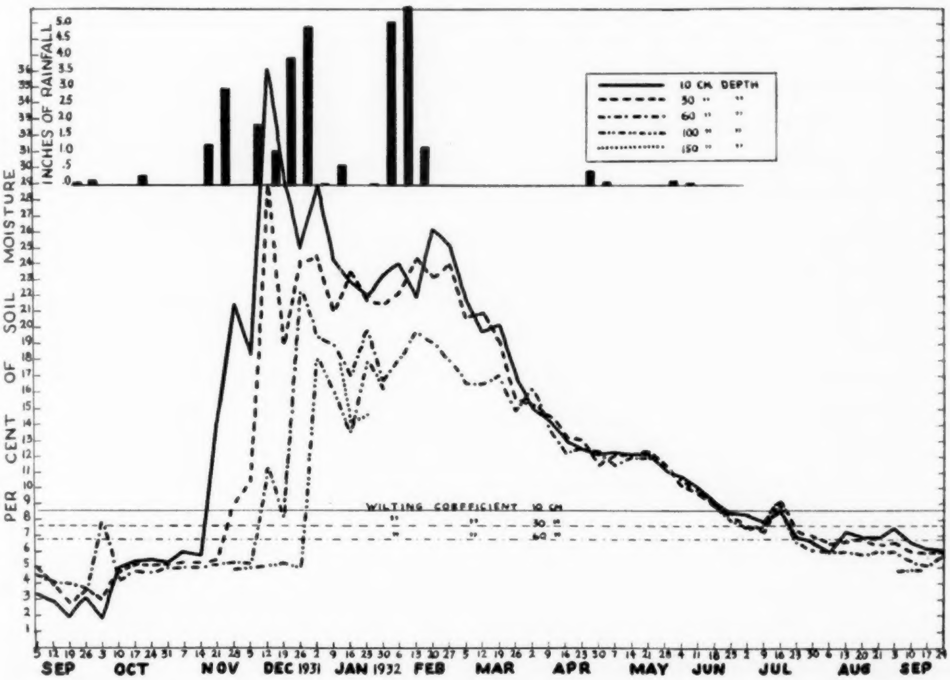

FIG. 12. Seasonal march of soil moisture at various depths, and other conditions in the chaparral. All data are for station 8, a northerly exposure at an elevation of about 2,300 feet.

and Hendrickson, 1928). The moisture equivalents and wilting percentages, like other edaphic conditions, were found to vary considerably, even within small areas where the vegetation was of fairly uniform character.

SEASONAL MARCH AND PENETRATION

The relations between precipitation, seasonal march, and penetration of soil moisture, and other features of soil moisture are shown in Figure 12. The graphs are plotted by weeks for a period of 13 months. All the graphs are for a single station (Sta. 8), but it is believed that this station represents fairly well the characteristic unburned chaparral of the area. The wilting coefficients for three soil levels are shown by horizontal lines.

Noticeable features are the extremely low content of moisture (3-5 per cent) in the soil during the dry summer months and the sudden increase (up to 30 per cent) in the surface level following the first substantial winter rains in November. The almost weekly rains maintained the moisture at somewhere near its field capacity during January and February.

The light rains at the beginning and end of the wet season made but very little change in the moisture content of the soil. The ineffectiveness of these first rains is shown by comparing the soil moisture graphs with the wilting coefficients. Although nearly half an inch of rain fell before the November storms, it did not raise the soil moisture above the wilting

coefficient, even at the 10 cm. depth, and the moisture from these rains did not, therefore, become available to the plants. Much of the light rains is intercepted by the vegetation and the layer of litter and humus material on the surface, and returned to the atmosphere by evaporation.

The slowness of the soil moisture below the 10 cm. depth to increase after the first heavy rains is significant. At the 30 cm. depth soil moisture rose a little during the first and second week following the rise at the 10 cm. depth but did not reach its field capacity until four weeks after the advent of the wet season. The soil at 60 cm. depth did not show any large increase in the moisture content until five weeks, and at the 100 cm. depth it remained as dry as in mid-summer until six weeks after the first heavy rains of the wet season. By the seventh week the water reached the 150 cm. level.

From these data it is apparent that, for the first meter of soil, even though the rains were heavy and frequent, water moved downward slowly, at the rate of only about 17 cm. per week. In coarser soil, penetration would be more rapid. The delay in the increase of the soil moisture in the lower strata means that, for the deeper roots, the dry season is some weeks longer, and the wet, or growing, season correspondingly shorter than for the surface layers. Cooper (1922, p. 46), who also observed the slow penetration of rain water, believed it was due to the air-filled condition of the soil.

A study of the intersection of the soil moisture graphs with the wilting coefficient lines shows that for roots more than one meter below the surface, there was no supply of readily available water until the first week in January, although heavy rains began about the middle of November and continued almost weekly. In ordinary situations in this chaparral most of the roots appeared to be near the surface, probably less than half a meter, and the plants had plenty of water for growth after the first ample rains. No evidence was found to show that root systems characteristically were especially extensive or deeply penetrating except where soil conditions were unusually inhospitable.

In contrast to the divergence of the graphs during the early part of the wet season, indicating wide differences in moisture content of the soil at the different depths, is the convergence of the graphs a few weeks after the last heavy rains of February, indicating uniformity of soil moisture at the several levels during the period when the soil was losing moisture most rapidly and when vegetative activity appeared to be at its highest rate. Apparently the plant roots absorbed moisture from each of these levels at about the same rate. There seemed to be but very little loss of water at this station (a northerly exposure) by direct evaporation from the surface of the ground, since the graph for the 10 cm. depth shows about the same

moisture content near the surface as at the deeper levels. This was probably due to retardation of surface evaporation by shade and ground litter.

During several months of the dry season, July to the middle of November, the moisture in the soil at the station being considered (Sta. 8) was below the wilting coefficient and the plants were, therefore, unable to get enough water for normal activities and were practically in a state of dormancy. During the 13 months considered here, soil moisture did not rise above the permanent wilting percentage until the latter half of November, and then at the 10 cm. depth only. The soil moisture at the 10 cm. depth dropped below the wilting coefficient in June, and at the 30 cm. and 60 cm. levels in the latter part of July. Thus for a period of about eight and a half months the plants were able to get water from at least one soil level. However, as will be pointed out later, another condition, namely, unfavorable temperature, was operative to prevent growth during the early part of this period.

The graphs in Figure 12 show a difference between the moisture content of the soil in September 1931 and September 1932. The average for the latter year was about 3 per cent higher than for the former year. In all probability this was due to the fact that the season previous to 1931 was below normal in rainfall whereas September 1932 followed a season above normal. These results are very similar to those obtained by Cooper (1922, p. 50) in the chaparral near Palo Alto, California, where the soil moisture content during the critical period following a season of deficient rainfall was very perceptibly lower than it was following a winter of abundant rain. The matter is of considerable significance because this initial moisture content determines how much water must enter the ground before the soil moisture is raised above the wilting coefficient and water becomes available for growth.

A comparison was made of the moisture content of the soil at Station 3, representing an area on which the chaparral had been recently burned, and at Station 4, located nearby in characteristic unburned chaparral. Both stations had southerly exposures. On the burned area the shrubs were sprouting from the root crowns, but much of the ground surface was bare, except during March and April when it was covered with a rather dense growth of herbaceous species. The results showed the moisture in the surface soil, 10 cm. level, varied approximately the same at both stations; in each case it dropped below the permanent wilting percentage in May. This depletion was due in part, especially on the burned area, to direct surface evaporation. At the 30 cm. level, however, the moisture situation was different at these two stations. On the unburned area, the soil moisture varied about as described for Station 8 above, dropping below its permanent wilting percentage near the end of July. At the 30 cm. depth on the

recently burned area, however, the moisture did not drop below its permanent wilting percentage at all, and averaged approximately 6 per cent higher than at Station 4 throughout the dry summer months, and had readily available water during this period. Apparently direct evaporation from the ground surface had little effect at this depth and the demands of the two-year-old shoots were not great enough to reduce the moisture to the permanent wilting percentage of the soil.

EVAPORATION

For the study of evaporation, there was set up at each station a battery of two or three Livingston white, spherical, porous cup atmometers equipped with the Livingston-Thone mercury-wool rain-correcting valves at the lower ends of the reservoir supply tubes in bottles of 1,000 cc. capacity. The porous cups, which were supported about 30 cm. above the ground surface, were cleaned weekly during the first year and restandardized at intervals of two or three months during the entire two-year period of investigation. All readings were corrected by the cup coefficients to the usual Livingston standard.

The atmometers were read weekly for 56 consecutive weeks, after which readings were made at four-week intervals to the end of the 104th week. The unbroken record of station readings for the entire period is probably rather remarkable in view of the number of instruments in service and the likelihood of disturbances by animals, man, and other agents. Some annoyance was caused by ants crawling through the air vent pipe, and, in a few cases during the second summer, by the growth of an unicellular green alga inside the glass reservoir supply tubes, but accuracy of the readings was probably not affected. A few of the cups were broken by the freezing of the contained water, but never all those at any one station, so that there was invariably at least one apparently valid reading at each station.

The coefficients of the cups changed but little during the progress of the work. Of the 32 new atmometer cups originally placed in service, 12, or 37.5 per cent, had undergone no change in their coefficients at the end of the first year, and eight, or 25 per cent, of them remained unchanged at the end of the second year. Individual cups were not in continuous use because of the periodic restandardizations.

SEASONAL MARCH

The most noticeable feature of the evaporation was its variability, the weekly readings usually showing a sharp rise or fall. In but a few cases only did the average daily evaporation for two consecutive weeks remain about the same for any one station, except at Station 1 which was markedly influenced by the proximity of the ocean.

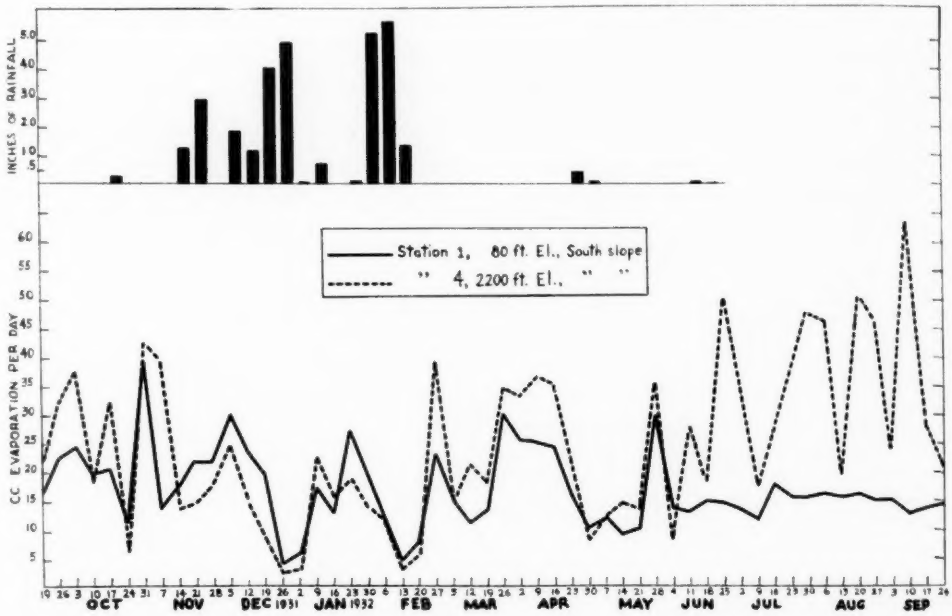

FIG. 13. Seasonal march of evaporation near the ocean and at an elevation of 2,200 feet.

. The quality of weekly evaporation rates in all seasons is shown by the graphs for two stations, namely, 1 and 4, in Figure 13. Station 4, located at an altitude of a little over 2,000 feet and several miles from the ocean, is believed to represent faithfully the characteristic chaparral of this area. Fluctuations in evaporation at all stations, except those close to the ocean, were similar to those at this one.

In the seasonal march of evaporation, as indicated by the graph for Station 4, peaks showing average daily evaporation of 35 cc. or more appeared eight times, once in October, once in February, and six times in the six months April to September. Of these peaks, two remained as such for two consecutive weeks, and one for four consecutive weeks, March 26 to April 16, the period of most rapid depletion of soil moisture. Extremes of low weekly evaporation rates occurred with somewhat less frequency. At only five points did the evaporation drop to a daily average of 10 cc. or less. These low points were most prominent in the wet months of December and February. The marked rise in January coincided with a period of low precipitation and the decided fall in May was related to the light rains of that time.

The seasonal tendencies of certain stations for both years of the investigation are tabulated in Table 7. The stations averaged together represent this chaparral well and have unbroken and complete records of readings for the entire period under discussion. The daily mean for the entire two years was approximately 25 cc. As would be expected, the evapora-

tion rates were lowest in winter and highest in summer. The monthly averages showed February to be the lowest month, with December and January but very little higher, and August the highest month with July and September almost as high. The single month with the lowest rate was December, 1931, with a daily average of 12.9 cc., and the single month with the highest rate was September, 1932, with a daily average of 37.6 cc.

TABLE 7. Tendencies in evaporation.

	Year 1931-32. Average of four stations (2, 4, 5, 8,)		Year 1932-33. Average of two stations (8, 15)		Average of both years	
	Total	Average daily	Total	Average daily	Total	Average daily
	cc. of water evaporated					
October	762.9	24.6	914.3	29.5	838.6	27.0
November	601.0	20.3	1020.4	34.0	810.7	27.0
December	401.8	12.9	695.4	22.4	548.6	17.7
Total	1765.7	19.2	2630.1	28.6	2197.9	23.9
January	522.1	16.8	544.5	17.5	533.3	17.8
February	399.1	13.2	589.5	21.0	494.3	17.3
March	729.2	23.5	783.0	25.3	756.1	24.4
Total	1650.4	18.1	1917.0	21.3	1783.7	19.6
April	753.0	25.1	803.0	26.8	778.0	25.9
May	516.5	16.6	699.0	25.6	607.7	19.6
June	703.2	23.4	838.0	28.0	770.6	25.7
Total	1972.7	21.7	2340.0	25.7	2156.3	23.7
July	830.5	26.8	1155.0	37.2	992.7	32.0
August	975.0	31.4	1031.2	34.5	1003.1	31.2
September	824.1	27.5	1052.0	37.6	938.1	31.2
Total	2629.6	28.6	3238.2	35.2	2933.9	31.9
Year	8018.4	21.9	10125.3	27.7	9071.8	24.8

For weekly periods, the lowest evaporation rate was at Station 6, where the average daily evaporation for the week of December 26 to January 2, 1931-1932, was 1.9 cc. The highest weekly rate for atmometers placed with their cups 30 cm. above the ground surface, was at Station 12, a westerly exposure at an elevation of 2,375 feet, where the average daily evaporation was 79.5 cc. for the week of September 3-10, 1932. At Station 13, a southerly exposure where evaporation was measured at the top of the vegetation, that is, 2 m. above the ground, a daily average of 90 cc. was recorded for the same week.

The evaporation conditions during the second year of the investigation were in some respects markedly different from those of the first. The evap-

oration in every month was higher during the second year than in the corresponding month of the first year, being greater by a daily average of 10 cc. or more for the months of November, December, July, and September. The daily average for the entire year, 1932-1933, was 5.8 cc. more than for the year 1931-1932. Thus evaporation, like precipitation, may vary considerably from year to year, the greater evaporation occurring during years of lower precipitation, thus increasing the unfavorability of the chaparral environment.

INFLUENCE OF THE OCEAN

A comparison of the two graphs in Figure 13 shows that the ocean had a very marked equalizing effect upon evaporation in the nearby vegetation. At Station 1, the sea-level station, evaporation during most of the year fluctuated in the same direction as it did at Station 4, representing the characteristic chaparral of higher elevations located several miles inland, but did not attain either such high or low extremes.

The most striking feature indicated in Figure 13, however, was the difference in evaporation at these two stations during the four summer months, June to September, 1932. During this period evaporation at the higher elevation station varied from an extreme low of 9 cc. as a daily average to a high rate of 64 cc., and the fluctuations were the most marked of any time of the year. Out of the 16 weeks of this period, evaporation was above a daily average of 45 cc. for six weeks and below 25 cc. for five weeks. On five occasions two consecutive weeks had a difference of 25 cc. or more as a daily average, one of these being a difference of 40 cc. In striking contrast to this was the low and almost uniform evaporation at the station near the ocean. The average daily evaporation for the entire period was only about 15 cc. and the variation from the lowest to the highest point was only 5 cc. Station 14, which was established February 20, 1932, about a quarter of a mile farther up the canyon from Station 1, and as a check upon this lower station, showed the same uniformity but ran consistently lower by a daily average of from 1 to 3 cc.

The records for Station 2, located about two miles from the ocean and at a well protected place within Topanga Canyon, still showed the influence of the ocean, though to a considerably lessened extent. The fluctuations at this "canyon" station were greater and both the high and low points were farther from the average than was the case closer to the ocean. These fluctuations, however, were by no means as marked as those described above for Station 4, at the higher elevation.

The indications are that conditions of low and uniform evaporation are found only on areas close to the ocean and in the canyons and deep ravines that extend a very few miles inland, and are not representative of evaporation in general in the chaparral of a coastal mountain range. All

of the stations located out of the canyon, and at an altitude of about 2,000 feet, exhibited comparatively high and much more variable evaporation rates.

INFLUENCE OF FIRE

It might be supposed that evaporation on recently burned areas, where much of the ground is bare and the atmometers were placed where the sun strikes them directly, would be considerably higher at all times than in a dense chaparral thicket where the atmometers are shaded nearly all the time. The differences found in this investigation, however, were not very marked. The fluctuations at Station 3, located on an area that had been burned one year previous to the beginning of the instrumentation, coincided with those in a nearby unburned chaparral with a similar southerly exposure, the amount of evaporation on the burned area being greater during most of the time but only by a little over 10 per cent for the year. The evaporation on the burned area was about 18 per cent greater than at Station 5, which had a northerly exposure.

The evaporation rate on the burned area was actually less than that on the nearby unburned area for a period of seven weeks, February 27 to April 9, 1932, with the exception of a single week. This period followed the end of the interval of heavy rains and coincided with the period of most rapid vegetative activity and depletion of soil moisture. At this time a rather rank growth of grasses and other herbs covered much of the ground of the burned area. The decreased evaporation rate at Station 3 was doubtless due largely to increased humidity caused by transpiration from the herbaceous vegetation surrounding the atmometers and also to breezes bearing the moisture of transpiration from the extensive herbage-covered slopes of the burned area. The evaporation rate at Station 3 might have been somewhat higher had the station been located farther from the edge of the unburned chaparral, this distance being about 25 feet. No evidence in favor of this possibility was noted, however, in the readings from Station 9, a second "burned chaparral" station established April 16, 1932, and located well removed from unburned vegetation. The indications were that the destruction of chaparral by burning did not seriously increase the intensity of evaporation.

INFLUENCE OF EXPOSURE

From the standpoint of evaporation, growth conditions are most favorable on north-facing slopes and least so on southerly exposures, this being especially the case during the critical months of the summer. The influences of slope exposure are illustrated graphically in Figure 14 for the six months, April-September, 1932. The graphs representing the northerly, easterly, westerly, and southerly exposures are based on the records of

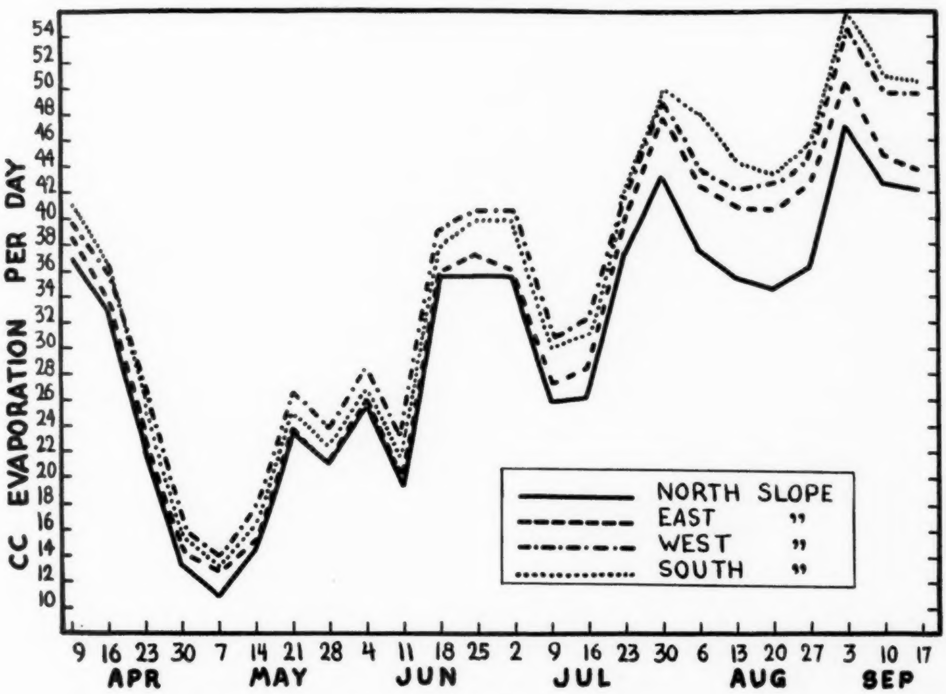

FIG. 14. The influence of slope exposure on evaporation.

Stations 8, 9, 12, and 13, respectively. All of these stations had approximately the same elevation of about 2,350 feet, and were located on different sides of the same hill (Fig. 2). None was protected by neighboring prominences, so that the differences in evaporation were apparently due entirely to the direction in which the slopes faced. In constructing the chart all the graphs were smoothed out somewhat by averaging three consecutive readings, thus: 1st, 2nd, and 3rd; 2nd, 3rd, and 4th; 3rd, 4th, and 5th; and so on. This simplifies the graphs and makes clearer those general tendencies which are most important in making such comparisons than are the absolute amounts of evaporation.

For the period plotted, the evaporation rate on the southerly exposure was consistently the highest and that on the northerly exposure the lowest, while on the westerly exposure evaporations were somewhat higher than on the easterly. The difference in the evaporation rates on the southerly and northerly exposures during the periods of low evaporation was not marked, being only about 2 or 3 cc. per day. The graphs are separated much more widely during the drier months of the summer. Computations show that for the three months, April to June, evaporation on the southerly exposure was about 10 per cent greater than on the northerly, but during the three months, July to September, it was about 20 per cent greater on the southerly.

EVAPORATION AT DIFFERENT LEVELS

For the purpose of comparing the evaporation rates at different levels in the chaparral, a standard for supporting atmometers above the ground was erected at Station 13, a southerly exposure with an elevation of 2,350 feet. One pair of atmometers was supported at the top of the vegetation, 2 m. above the ground where they were unshaded at all times; a second pair near the middle of the foliage mass, 1 m. above the ground; and a third pair was placed on the ground in the same way as at all other stations. The apparatus is shown in Figure 10. The vegetation at this station was about 60 per cent *Adenostoma fasciculatum.*

The highest rate of evaporation was found at the top of the vegetation and the lowest at the middle level. The readings of the ground atmometers were consistently higher than those of the one-meter level in spite of denser shade at the ground level. This was doubtless due in part to greater amounts of moisture transpired at the middle level, and, in part, to the fact that temperature at the ground level was slightly higher. From the summarization of Table 8, it is apparent that, taking the evaporation at the top of the vegetation as 100, the ratios of the top, middle, and ground levels were 100:83:86, respectively.

It might be supposed that the higher evaporation at the top of the vegetation was due to higher temperatures, since the atmometers here were unshaded. Such, however, was not the case, as a series of temperature readings showed the temperature at the top to be decidedly lower, by an average of about 3° C., than at the lower levels. The temperature at the ground level averaged about 1° higher than at the middle level. The temperatures were taken at various times during July and August and each figure for temperature given in Table 8 is an average of over twenty readings. No exceptions to the relative order of temperatures given were recorded, and it is therefore believed that the relation of temperature at different levels as stated, may be a general one for these summer months.

In view of the lower temperatures at the top of this vegetation it is not certain why the evaporation there should be higher by about 20 per cent.

TABLE 8. Evaporation rates and temperatures at different levels at Station 13 for a period of twenty-eight weeks in the spring and summer, April 9 to September 24, 1932.

Height above ground	Evaporation in cc.		Evaporation ratio	Temperature, degr. C. Av. of readings	Temperature ratio
	Total for period	Average daily			
Surface	6857.1	35.0	86.	35.2	100.0
1 meter	6603.3	33.7	83.	34.2	97.2
2 meters	7946.4	40.5	100.	31.9	90.7

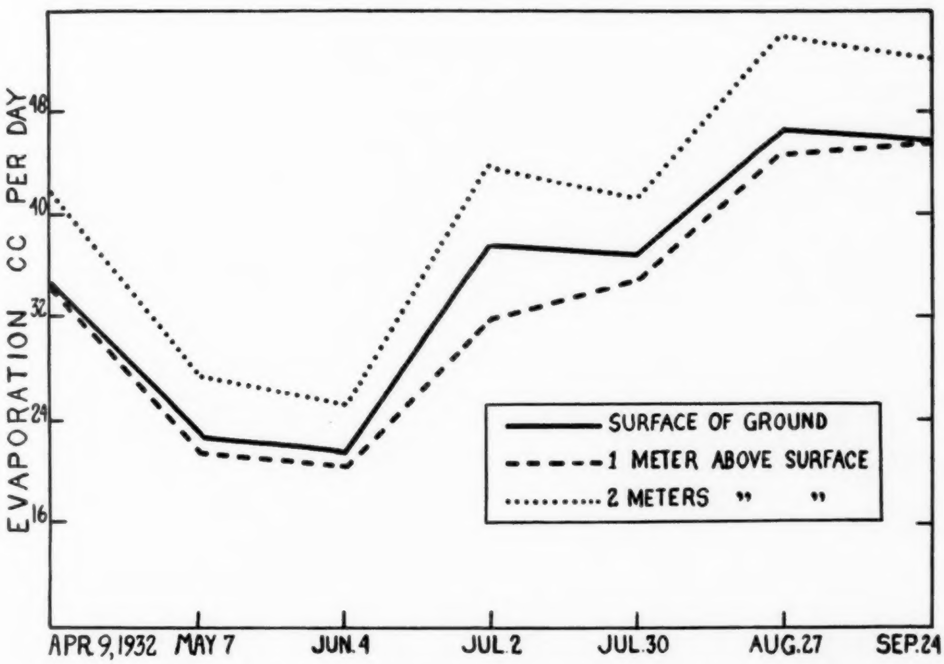

FIG. 15. Evaporation in the chaparral at different levels above the ground. All data for Station 13, a southerly exposure at an elevation of about 2,350 feet.

Solar radiation is probably unimportant since white cup atmometers were used. Air movement probably accounts for much of the increase. Wind movement is less in the vegetation than over its top, and the vapor resulting from transpiration is not removed so readily, thus tending to increase the humidity and decrease the evaporation within the foliage mass. The main features of evaporation at different levels are shown in Figure 15.

EVAPORATION AND RADIATION

For a period of six weeks, February 11 to May 25, 1932, two black cup atmometers were maintained close to the two white ones at Station 9, in the recently burned area. During the six weeks period following this, April 1 to May 6, the black cup atmometers were placed beside the white ones at Station 8, in characteristic unburned chaparral on a northerly slope. This apparatus constituted a so-called radio-atmometer, for the approximate measure of the influence on evaporation of the impinging radiation from sun, sky, and earth. The greater evaporation from the black cups is due chiefly to the drying influence of radiation, the chief component of which is direct sunshine. The difference in the corrected readings of the black and white cups is, therefore, a measure of the effective intensity of radiation (Livingston, 1935, p. 469).

At Station 9 the evaporation as measured by the black cups was about 19 cc. per day more than that measured by the white cups, an average in-

crease of 66 per cent for the six weeks considered. At Station 8, however, during the following six weeks, the evaporativity exceeded the evaporating power of the air by about 8 cc. per day, an increase of only 44 per cent. In this case the lower light intensity in an ordinary stand of chaparral appeared to reduce the influence of radiation on evaporation by about 11 cc. of evaporation per day. It should be noted, however, that the general evaporation for the second six-weeks period here considered was considerably lower than that during the first six-weeks period. This fact might have had some effect upon the results.

SATURATION DEFICIT, RELATIVE HUMIDITY, SOIL TEMPERATURE

Saturation deficits were calculated from cog psychrometer readings made at intervals of two or three months throughout the first year of the investigation. These discontinuous readings made at irregular intervals are of value in making comparisons of the atmospheric conditions at the several stations. On the days when these observations of humidity were made the stations were visited as rapidly as possible, so that all the readings were made during a period of not much over one hour, this being shortly before noon. The data for six stations are summarized in Table 9.

The stations in Topanga Canyon, especially those near the ocean, as would be expected, were found to be the most humid and to have the least fluctuation. The saturation deficit at Station 1, the sea-level station, averaged 3.9 mm. for the six readings made at various times during the year. Station 2, located about two miles up the canyon from the ocean and at an elevation of 400 feet, had an average of 4.9 mm. At Stations 3, 4, 5, and 8, all of which were located along ridges at elevations of about

TABLE 9. Saturation deficit in mm. of mercury pressure and relative humidity in percentage. Numbers in parentheses are the humidities. 1931-1932.

Station	Elevation	Nov. 7	Nov. 28	Feb. 20	May 28	Aug. 20	Sept. 24	Average
1..........	85	2.9 (82.5)	3.3 (71.0)	3.7 (73.0)	3.4 (80.0)	5.5 (76.5)	4.9 (75.0)	3.9
2..........	400	3.9 (78.0)	3.5 (72.0)	4.5 (66.0)	4.4 (73.0)	8.0 (67.0)	5.4 (72.0)	4.9
3..........	2150	8.8 (53.0)	3.0 (69.0)	3.4 (71.5)	1.8 (85.0)	22.4 (30.0)	25.2 (36.0)	10.8
4..........	2150	8.2 (56.0)	2.5 (70.0)	4.3 (66.5)	1.8 (85.0)	22.7 (28.0)	25.4 (35.0)	10.8
5..........	2200	8.5 (53.0)	2.2 (71.0)	3.0 (73.0)	1.7 (85.0)	24.6 (29.0)	18.5 (33.0)	9.7
8..........	2350	8.2 (55.0)	2.2 (71.0)	3.6 (67.0)	2.5 (79.5)	23.4 (25.5)	20.4 (34.0)	10.5

2,000 feet, the average deficit was 10.5 mm., being, thus, more than twice as arid as the canyon stations closer to the ocean. This rather sudden decline in humidity with altitude and distance from the ocean, seems to indicate that the direct equalizing effect of the ocean on atmosphere moisture is confined to a rather narrow coastal strip and, for a limited distance, to the canyons that extend away from it.

The differences in saturation deficit on different exposures were not great. An average of four readings, two northerly slopes (Station 5 and 8) had a deficit of 12.2 mm. while two southerly slopes (Station 4 and 13) had 14.5 mm. The variations at a given place, however, were considerable from time to time. At Station 4, for example, the saturation deficit varied from 1.8 to 25.4 mm.

A study of hourly readings of relative humidity made at various places in the Santa Monica Mountains by the Los Angeles County Forestry Department showed striking differences in the humidity between canyon slope and mountain peak, and rapid fluctuations from time to time at a given place. During the summer period, June 18 to September 24, 1932, the average relative humidity on Castro Peak (elevation 2,819 feet) was about 45 per cent, while at Malibu Headquarters (elevation 747 feet) in Topanga Canyon it was about 72 per cent for the same period, being surprisingly high for the hot dry months. The records also show that, as an average for the three years 1931-1933, the relative humidity at Malibu Headquarters was over 3 per cent higher during the month of July than it was during January. The unexpected humidities at this station are doubtless due to its well-protected locations near the bottom of Topanga Canyon and to moisture-laden breezes moving up the canyon from the ocean. Humidities taken in less protected places were more like those for Castro Peak mentioned above, and are much more representative of the chaparral in general.

Soil temperatures were taken at the same time as the soil samples, by thrusting the bulb of a chemical thermometer in the wall of a freshly cut trench. Soil temperatures for two levels, 10 cm. and 30 cm. are shown in Figure 16 for three stations, 3, 4, and 8, from February to September, 1932. The north slope station (Sta. 8) ran consistently the lowest. The temperatures were considerably higher on the burned area, especially during the summer months. Temperatures at the 10 cm. level fluctuated much more than did those at the 30 cm. level.

Air temperatures in this area seldom drop below the freezing point for more than a very brief period of time, as shown by the fact that only a few of the atmometers were broken by the freezing of the contained water although the instruments were exposed continuously for two years.

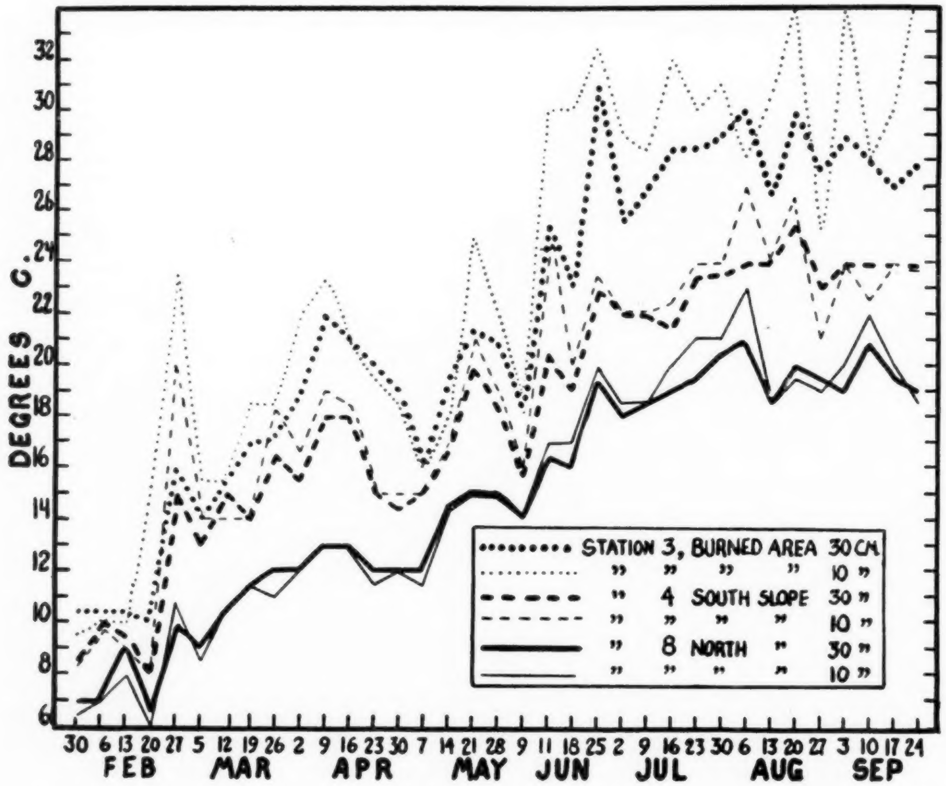

FIG. 16. Soil temperatures at stations representing different conditions in the chaparral.

INTERRELATION OF FACTORS

GROWING SEASON

In a region with winters so mild that temperatures seldom reach the freezing point it might be conjectured that the growing season for native vegetation would coincide with the period during which water is readily available. If this were true, the growing season could be calculated theoretically from soil moisture and permanent wilting percentage data. It was previously pointed out that water was readily available from the middle of November to the end of July, a period of about eight and a half months or two-thirds of the year. Noticeable activity on the part of the plants, however, was restricted to a much shorter period. There was practically no external evidence of plant activity during November and December, 1931, and in January, 1932, the only evidence of growth was the flowering of a very few species. Since these are the coldest months, it is apparent that the temperatures are low enough to greatly restrict the absorption of water by roots, and other plant activities, so that growth could not continue and the real growing season does not, therefore, start until both soil and air tempera-

tures have risen to a favorable minimum. This is in accord with the conclusions of Maximov (1929, p. 83) in his discussion of the influences of temperature on water supply.

In order to procure more exact evidence as to the beginning, height, and end of the growing season than could be obtained from phenological observations, a series of measurements of the increase in length of certain stems was made. In doing this, three or more stems of normal appearance on plants of the chosen species were marked near the tip with waterproof ink, and measurements of any increase in length were made on the occasion of the regular weekly visit to the stations. Numerous accidents happened to the marked stems but enough of them remained intact to give significant information. Most of these were on stump sprouts at the edge of the burned area near Stations 3 and 4 where growth conditions were doubtless better than in the unburned chaparral. The graph for stem elongation shown in Figure 17 represents the average weekly growth of three species, *Adenostoma fasciculatum, Rhus laurina,* and *Photinia arbutifolia.*

Inspection of the graph shows that a small amount of stem elongation growth occurred in the fall, about the latter part of November or early December. No further growth in length was recorded until the latter part of February when it began rather suddenly and continued until about the first of July. Following this, elongation decreased and ceased entirely about the middle of July. The most rapid growth occurred during the latter part of March and the first part of April.

During the second year of this investigation the measurements of stem elongation at Station 3 were repeated and additional stems representing the same and other species were measured at Stations 9, 14, and 15, the last two representing characteristic unburned chaparral. The average elongation of over 20 stems of five different species was just about the same as in the first season. The most noticeable difference was the fact that elongation persisted somewhat longer into the summer, due, no doubt, to the lateness of the spring rains.

These data are not intended to constitute a complete quantitative record of growths at the ends of the marked stems. They are employed here only for the clues they supply as to the salient features of the growing season. The weaknesses inherent in the method are recognized. The series of measurements might well have included a greater number of species from the unburned chaparral. Nevertheless, it is believed the results approximate fairly well the significant responses made by the plants to the growing conditions.

From a consideration of the observations made during the two years of this investigation, it may be concluded that the characteristic events of the ordinary growing season are about as follows. There is a short and relatively unimportant period of growth in the fall, after the advent of the

first rains and while temperatures are still favorable. This is followed by a month or more of inactivity, due to low temperatures. The beginning of flowering comes in January and continues in different species until midsummer. A period of rapid vegetative growth occurs in March and April followed by a period of lowered growth rate in May and June. After this vegetative activity diminishes and ceases entirely in July.

MOISTURE RATIO

Since moisture conditions constitute the critical feature of the chaparral environment, it is desirable to use a single numerical value to express this factor as comprehensively as possible. For this purpose various ratios may be employed. A rainfall-evaporation ratio (R/E) has sometimes been used, but this is not suitable for southern California on account of the peculiar distribution of the precipitation, one in which most of the rain falls in a single or a very few months, while in other months there is little or none. Thus this ratio applied to the Santa Monica Mountains would indicate very poor moisture conditions in March and April, a time when the plants are actually making their most rapid growth.

An evaporation-soil moisture (E/SM) ratio, which brings together the most important factors of both the atmosphere and soil, much more adequately represents the favorability or unfavorability of growth conditions in southern California. Shreve (1927, p. 409) employed this ratio in Arizona and California. In the present investigation it was found that the most favorable E/SM ratios, those of about 1.0, existed during December, January and February, and that during March, April and May they averaged about 2.2, being only slightly less favorable. In June and July the ratios, averaging about 4.0, indicated severe moisture conditions, and in August and September they showed extreme conditions, averaging about 5.5. The highest ratio found was one of 7.0 in September. The E/SM ratios for the second year of the investigation were remarkably similar to those of the first, in spite of the fact that the precipitation was quite different.

The Relation of Factors to Each Other and to the Growth of Stems in Length

For the purpose of presenting in conjunction those features of the environmental complex that have been considered, and to indicate something of the relation of the environmental complex to chaparral, all the important moisture factors for the year 1931-1932, including precipitation, soil moisture, wilting coefficients, and evaporation, have been brought together, with soil temperature and the growth of stems in length, in a single chart (Fig. 17). Herein the data are plotted on a weekly basis for 56 consecutive weeks. All of the data are based on averages of four selected stations,

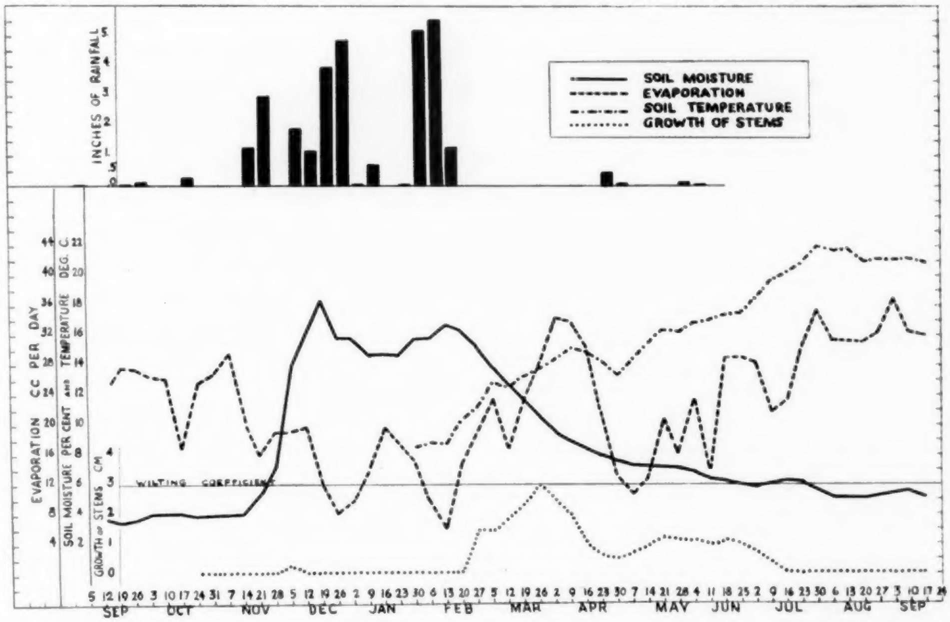

FIG. 17. Interrelations of the physical conditions in the chaparral habitat, and the growth of plants as represented by stem elongation. Each graph is somewhat smoothed and is plotted from data averaged for four stations.

numbers 2, 4, 5, and 8. Of these, two were northerly and two southerly exposures. Three of the stations were at elevations of a little over 2,000 feet, and the fourth was in a canyon at an elevation of 400 feet. It is believed that this selection faithfully represents general conditions in the chaparral of the Santa Monica Mountains. All of the graphs in the figure have been smoothed out by the method described on page 439 in order that the major tendencies might be more apparent.

Some of the features shown in Figure 17, such as the relation between precipitation and soil moisture, the rapid fluctuation of evaporation, and the increase in soil temperature, have been previously considered as they applied to certain individual stations. The limitation in the length of the growing season imposed by the availability of water is marked by the intersections of the soil moisture and wilting coefficient graphs. Thus it may be seen that, for the year 1931-1932, water was available from the latter part of November until the end of July, a period of about eight and one-half months. The figure shows that there was a striking lack of agreement between soil moisture and evaporation conditions in that, during much of the period when soil moisture was abundant, evaporation was very low, indicating that some of the factors influencing evaporation were not favorable to plant activity. Evaporation measurements express in large measure the effects of temperature, relative humidity, and wind. It is probable that temperature is the effective factor in restricting plant growth during periods of low evap-

oration, since the temperatures recorded for the period of plant inactivity studied were lower than those for any other time, whereas wind movement for this period was not unusual, and it is not probable that the comparatively high humidities inhibited growth. The soil temperature graph shows that the temperature of the soil increased rather steadily from about 8° C. in January to 22° C. in July. The upward trend of the soil temperature graph is rather similar to that of evaporation but it steadily diverges from that of soil moisture. It may be noticed that stem elongation did not begin until the temperature of the soil rose above 10° C.

The relations of the graph of stem elongation to those of the physical conditions are significant. The small amount of growth that occurred in early December, was after the first substantial rains and before evaporation dropped below 16 cc. per day. No further elongation of stems occurred until the end of February, when evaporation increased to more than 16 cc. per day. The temperature of the soil at this time, the latter part of February, had risen above 10° C. The average weekly elongation of stems of the selected plants was comparatively rapid for a period of eight weeks, February 27 to April 16, attaining a maximum of 3 cm. per week at the end of March. By the end of April, stem elongation had dropped to 0.5 cm. per week. Then it increased again to an approximate average of 1 cm. per week in May and June, after which it decreased, and in the early part of July ceased entirely.

All growth phenomena of plants are not, of course, represented in stem elongation. In the year 1932-1933 Arctostaphylos was in full bloom in January, seven or eight weeks before stems had begun to elongate, and *Rhus laurina* was still blooming in July a few weeks after stem growth had stopped. Nevertheless, the period of most rapid stem elongation doubtless indicates a time when the complex of environmental conditions is especially favorable for plant activity, and it may be when they average best for physiological processes.

During the period when stem elongation was most rapid, March and April, the evaporation and soil temperature conditions were moderate and the decreasing supply of soil moisture still averaged 5 or 6 per cent above the permanent wilting percentage. In April the soil moisture averaged about 2 per cent, and in May about 1 per cent, above the wilting coefficient. In July, when stem elongation stopped and the flowering of a few species was the only visible activity of the plants, soil moisture remained close to the wilting coefficient.

The relations between the fluctuations of the stem-elongation graph and the evaporation graph are curious. It is probably more than coincidence that most of the noticeable increases in elongation followed one or two weeks after a drop from a somewhat high to a moderate or medium weekly evap-

oration rate and, conversely, that the decreases in the elongation rate followed increases of the evaporation rate. The large decrease in the rate of stem elongation in April followed a rather sustained period of high evaporation, during which the average daily evaporation was 30 cc. or higher, and during which both soil moisture and soil temperature were favorable. During such a period of high evaporation it is likely that the loss of water from the plant due to rapid transpiration is so great as to interfere with the normal physiological processes of the plant and to retard its rate of growth.

During the succeeding year, 1932-1933, the chief relations just illustrated as existing between soil moisture, soil temperature, and stem elongation for 1931-1932, were found to prevail again, the differences being of minor importance. Somewhat more stem elongation occurred in the autumn of 1932 than in the previous year. This may have been due to the fact that the initial soil moisture content was about 2 per cent higher than at the beginning of the first year and consequently less rain was needed to bring it the wilting coefficient.

From a consideration of the correlations presented it appears that the most important conditions in the chaparral environment are the moisture relations, the effects of which are influenced somewhat by the low, but seldom freezing, temperatures of the winter months. The most critical period is the late summer, August and September, and that part of the autumn which precedes substantial rains. At this time the soil moisture is below the permanent wilting percentage and the high evaporation causes serious losses of water from plants.

Local variations in the physical conditions are caused by topographic features such as the proximity of the ocean, slope exposure, slope gradient, and altitude. The effects of these are reflected in minor changes in the structure of the vegetation, but the ecological type of chaparral is not markedly altered since it may be observed to spread in an almost unbroken mantle over the mountain complex. Occasionally, as at the bottom of a canyon or deep ravine, moisture conditions make possible the growth of trees, and here the chaparral gives way to the closely related broad-sclerophyll woodland. In other limited areas, as at the base of the mountains on either side of the range, there is not enough available water to support characteristic chaparral and the more xeric coastal sagebrush appears.

The advantages of the evergreen sclerophyll habit that is so characteristic of chaparral have been described by Schimper (1903, p. 513) and Cooper (1922, p. 66). The ever-present photosynthetic apparatus makes it possible for the plants to utilize warm periods in the winter and early spring months for food synthesis, when other plants have no leaves or are expending energy in making them. Thus an effective growth can be made

before the soil moisture drops below the permanent wilting percentage in the summer.

From the data obtained in this investigation, there is little reason to believe that shoot-growth activities during the winter months are important, but it is obvious that a vigorous flowering and vegetative activity starts without delay as soon as the temperatures of air and soil have risen above the minima necessary for these physiological processes. The sclerophyllous habit, which is chiefly due to the heavy layer of cutin, thick epidermis, and compact mesophyll, is an effective aid in conserving the scanty supplies of moisture during the critical period from August to October or November, so that, despite large transpiring surfaces, enough water is absorbed by the roots to maintain the necessary physiological processes at low rates.

The reason for the marked uniformity in size and general appearance of chaparral plants is not clear. Trees are doubtless excluded because of insufficient soil moisture, and smaller shrubs and herbs are probably kept out by the shade of the dense broad-evergreen leaves. In view of the taxonomic diversity of chaparral areas, however, more variation in the height of the shrubs might be expected. Wind, through its desiccating influence, may be a factor in preventing branches from growing more than slightly above the general level of the vegetation. Attention has been called to the fact that evaporation at the top of the vegetation on a southerly slope exposure was about 20 per cent greater on the average for a period of 28 weeks, April 9 to September 24, 1932, than it was at 1 m. lower, i.e., within the foliage mass. Thus a branch growing much above the general level of the vegetation would be subjected to the handicap of much greater desiccation and might not be able to continue its development. In the proximity of the beach, where vegetation is unprotected from the direct sweep of ocean winds, thickets, which may be composed of half a dozen species, are so even on the top as to give the appearance of having been artificially trimmed. Wind alone, however, does not appear to be an adequate explanation for the uniform heights of chaparral shrubs as they are found growing generally over wide areas embracing diverse situations.

SUMMARY

1. An intensive instrumental investigation during the two years 1931-1932 and 1932-1933 was made of the vegetation, chiefly chaparral, and the physical conditions, especially soil moisture and evaporation, of a representative area of the Santa Monica Mountains, California.

2. The flowering period of most chaparral species was of only a few weeks duration, but flowering activity continued among the various species for over half the year, the greatest wave of blossoming activity came in the latter part of March and in April.

3. *Adenostoma fasciculatum*, the most abundant species, was found to constitute 38.6 per cent of all the vegetation touching the line transects and to cover 57 per cent of the total distance of the transect lines run in various places. The species of second greatest abundance was *Ceanothus macrocarpus* which constituted 16.5 per cent of the vegetation and covered 24.5 per cent of the transect distance. *Salvia mellifera*, an important species in the coastal sagebrush, constituted 9.5 per cent of the vegetation, but the plants usually occurred underneath the taller sclerophyllous shrubs and were often not in control of the ground. In such situations this species is probably a remnant of a seral community that appeared after fire.

4. Southerly exposures were found to have nearly 60 per cent *Adenostoma fasciculatum*, but northerly ones only about 25 per cent. *Quercus dumosa* constituted about 15 per cent of the vegetation on northerly slopes, but very little of this species occurred on other exposures. The overlapping or interlacing of branches of chaparral shrubs was computed to be 58 per cent on northerly but only about 31 per cent on southerly exposures.

5. In this area more than 90 per cent of the rain normally falls during the six months, November to April, and the summer months are practically rainless. During the years of this investigation, it was found that the precipitation within the mountainous area was nearly 50 per cent greater than close to the ocean and that 20 per cent more rainfall was recorded on northerly and easterly exposures than on southerly and westerly ones. Measurements indicated that about one-third of the light rains of the early and late portions of the wet season was intercepted by the vegetation, the plants with larger broader leaves intercepting more than others. This may account in part for the greater success of the narrow-leaved *Adenostoma fasciculatum*.

6. Soil moisture was available to plants for a period of about eight and one-half months, November to July. Penetration in a fairly fine-textured soil was slow, six weeks being required for the moisture to reach a depth of 1 m. although substantial rains occurred almost weekly. After the end of the period of heavy rains, soil moisture decreased uniformly at all levels. On an area where the chaparral had been recently destroyed by fire, the water content at the 30 cm. level was above the permanent wilting percentage throughout the year, thus indicating that the vegetation is chiefly responsible for the depletion of soil moisture rather than direct surface evaporation.

7. Evaporation, as measured by Livingston white porous cup atmometers, was found to fluctuate greatly, the rate seldom remaining high or low for more than two consecutive weeks. The average rate for all seasons was 25 cc. per day. During the dry season the evaporation rates near the ground (30 cm. level) exceeded 50 cc. per day on a number of

occasions and attained an extreme high rate of nearly 80 cc. per day. The ratio of evaporation at the top of the vegetation (2 m. level), middle of foliage mass (1 m. level), and near the ground surface (30 cm. level) was 100:83:86. The considerably higher rate at the top of the vegetation is interesting in view of the fact that the temperatures there averaged about 3° C. lower during July and August. Evaporation on an unshaded recently burned area was found to be higher by 10 per cent than on characteristically unburned areas nearby.

8. On a recently burned area, evaporativity, as measured by Livingston black porous cup atmometers, was found to be 66 per cent greater than the evaporating power of the air as measured by the white porous cup atmometers, but in the shade of the characteristic chaparral on a northerly exposure the evaporativity was only 44 per cent greater.

9. Atmospheric moisture, as shown by determinations of the saturation deficit and relative humidity, varied rapidly from time to time and place to place. The average saturation deficit close to the ocean was 3.9 mm. for a number of readings made at various times throughout the year, but at elevations of about 2,000 feet and about three miles inland it was 10.5 mm., showing conditions considerably more than twice as arid. On the peaks, the relative humidity during the summer months averaged about 45 per cent as compared with 72 per cent in Topanga Canyon.

10. Soil temperatures at a depth of 10 cm. fluctuated considerably but there were no especially rapid changes at depths of 30 cm. and 60 cm. The deeper levels were very slightly warmer in winter and slightly colder in the summer than near the surface. At a depth of 30 cm. the temperature of the soil averaged less than 10° C. in February and between 18 and 28° C. in August and September. Air temperatures during the winter months occasionally dropped slightly below the freezing point for short periods.

11. The most active period of growth, as expressed by measurements of stem elongation, was March and early April when the soil contained an abundance of available water and the soil temperature was above 10° C. Stem elongation continued at decreasing rates through May and June and stopped entirely about the middle of July when soil moisture dropped below the permanent wilting percentage. A small amount of stem elongation took place in the autumn but none during the early portion of the winter when temperatures were low. There was fairly good correlation between stem elongation and an evaporation-soil moisture ratio (E/SM) in the latter, but not the earlier part of the growing season.

12. Wind may be a factor in causing the striking uniformity in the height of chaparral shrubs, in that it greatly increases the severity of evaporation just above the general level of the vegetation.

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LITERATURE CITED

Abrams, L. R. 1910. A phytogeographic and taxonomic study of the southern California trees and shrubs. *Bul. N. Y. Bot. Garden*, **6**:300-485.

Briggs, L. J. and H. L. Shantz. 1912. The wilting coefficient for different plants and its indirect determination. *U. S. Dept. Agr. Bur. Plant Indus. Bul.* **230.**

Clements, F. E. 1920. Plant indicators: the relation of plant communities to process and practice. *Carnegie Inst. Wash. Pub.* **290.**

Cooper, W. S. 1922. The broad-sclerophyll vegetation of California: an ecological study of the chaparral and its related communities. *Carnegie Inst. Wash. Pub.* **319.**

Copeland, E. B. 1932. Transpiration by chaparral and its effect upon the temperature of leaves. *Univ. Calif. Pubs. Bot.* **17**: 1-21.

Hall, H. M. 1902. A botanical survey of San Jacinto Mountain. *Univ. Calif. Pubs., Bot.*, **1**: 1-144.

Hoots, H. W. Geology of the eastern part of the Santa Monica Mountains, Los Angeles County, California. *U. S. Geol. Survey Prof. Paper* **165 C.**

Howell, J. T. 1929. The flora of the Santa Ana Canyon region. *Madroño*, **1**:243-253.

Jepson, W. L. 1910. The silva of California. Berkeley, California.

——— 1925. A manual of the flowering plants of California. Berkeley, California.

Leiberg, J. B. 1899. San Bernardino forest reserve. *U. S. Geol. Survey 19th Ann. Rpt.* (pt. 5) : 359-365.

Livingston, B. E. 1935. Atmometers of porous porcelain and paper, their use in physiological ecology. *Ecology*, **16**: 438-472.

Lowdermilk, W. C. 1933. Provisional working plan for watershed and water conservation study in the chaparral region of California. *Calif. Forest Expt. Sta.* (Mimeographed paper).

Maximov, N. A. 1929. The plant in relation to water. Edited by R. H. Yapp. New York.

McKenney, R. E. B. 1901. Notes on plant distribution in southern California, U. S. A. *Beih. Bot. Centbl.* **10**: 166-178.

Nelson, J. W. et al. 1920. Soil survey of the Ventura area, California. *U. S. Dept. Agr. Bur. Soils and Univ. Calif. Agr. Expt. Sta.*

Parish, S. B. 1903. A sketch of the flora of southern California. *Bot. Gaz.* **36**:203-222, 259-279.

Russell, E. J. 1926. Climates of California. *Univ. Calif. Pubs. Geogr.* **2**: 73-84.

Schimper, A. F. W. 1903. Plant geography upon a physiological basis. Trans. by W. R. Fisher. Ed. by P. Groom and I. B. Balfour, Oxford, England.

Shapiro, A. A. and H. de Forest. 1932. A comparison of transpiration rates in chaparral. *Ecology*, **13**: 290-295.

Shreve, F. 1927. The vegetation of a coastal mountain range. *Ecology*, **8**: 27-44.

——— 1927. The physical conditions of a coastal mountain range. *Ecology*, **8**: 398-414.

Turner, S. 1934. Annual report for fiscal year ending June 30, 1934. Los Angeles County (Calif.) Forestry Dept.

Veihmeyer, F. J. and A. H. Hendrickson. 1928. Soil moisture at permanent wilting of plants. *Plant Physiol.* **3**: 353-357.

Whitfield, C. J. 1932. Ecological aspects of transpiration. II. Pike's Peak and Santa Barbara regions: edaphic and climatic aspects. *Bot. Gaz.*, **94**: 183-196.

——— 1932. Osmotic concentration of chaparral, coastal sagebrush and dune species of southern California. *Ecology*, **13**: 280.